VEGETATION ASSOCIATIONS ALONG DISTURBANCE GRADIENTS ON THE SAND DUNES OF SABLE ISLAND, NOVA SCOTIA

A Thesis Submitted to the College of Graduate Studies and Research

In Partial Fulfillment of the Requirements

For the Degree of Master of Science

In the Department of Biology

University of Saskatchewan

Saskatoon

By

EMILY JOAN TISSIER

PERMISSION TO USE AND DISCLAIMER STATEMENT

In presenting this thesis in partial fulfillment of the requirements for a graduate degree from the University of Saskatchewan, I agree that the Libraries of this University may make it freely available for inspection. I further agree that permission for copying of this thesis in any manner, in whole or in part, for scholarly purposes may be granted by the professor who supervised my thesis work or, in their absence, by the Head of the Department or the Dean of the College in which my thesis work was done. It is understood that any copying or publication or use of this thesis or parts thereof for financial gain shall not be allowed without my written permission. It is also understood that due recognition shall be given to me and to the University of Saskatchewan in any scholarly use which may be made of any material in my thesis.

Requests for permission to copy or to make other use of material in this thesis in whole or part should be addressed to:

Head of the Department of Biology
University of Saskatchewan
112 Science Place
Saskatoon, Saskatchewan, S7N 5E2

ABSTRACT

Sable Island, Nova Scotia, is a dynamic dune ecosystem that is composed of plant communities exposed to varying levels of disturbance. The island is exposed to extreme weather events throughout the year, and this plays an important role in dune succession; however, the vegetation dynamics of this ecosystem are poorly understood. I investigated plant community responses to natural disturbance gradients using field measurements of community composition, abiotic variables, and grazing (and/or browsing) pressure from the island's population of feral horses. Sampling plots were distributed across the entire island using a stratified random sampling design to capture the maximum range of environmental gradients and vegetation types. I measured species composition at each site in combination with predictor environmental variables: slope, organic layer presence, distance from shore, and evidence of grazing. I identified three different vegetation assemblages via hierarchical cluster analysis and non-metric multidimensional scaling ordination, and examined their associations with different environmental conditions and plant traits. Multivariate analyses indicated a strong relationship between community composition and distance from shore. Slope was the most important variable affecting whether a plot had vegetation and instances of grazing. Species with traits better suited to withstand sand burial and salt spray were present in areas closer to shore. Areas with less disturbance contained more shrub and heath communities. Evidence of grazing was present in all vegetation types with no observed relationship to plant species composition. Dune succession on Sable Island was not linear and is better described as the vegetative response to dynamic environmental stress rather than the result of gradual soil development and competitive displacement.

ACKNOWLEDGEMENTS

Thank you to Jill Johnstone who believed in me and gave me opportunities when others would not. Her guidance, high standards, encouragement, and friendship have made me a better scientist and person. I thank Phil McLoughlin, my co-supervisor, who gave me the opportunity to study on Sable, provided crucial feedback, and taught me how to include animals in my ecological thought process. As a member of my committee, John Sheard gave thoughtful advice in all aspects of planning, field work, analysis, and writing. I am grateful to my external examiner, Darcy Henderson, whose comments have contributed greatly to improving the final version of this thesis.

This project was funded by the Natural Sciences and Engineering Research Council of Canada (NSERC) and a University of Saskatchewan teaching fellowship. In-kind and logistical support was provided by Fisheries and Oceans Canada including Canada Coast Guard, the Bedford Institute of Oceanography (DFO Science), and Environment Canada. Thank you to the Canadian Coast Guard for granting us permission to go to Sable Island. I am especially thankful for Gerry Forbes and the staff of the Sable Island weather station for all their logistical and mechanical help; as well as Maritime Air for safe travels on and off the island.

Thank you to Adrienne Contasti and Kenton Lysak for their help and good company in the field as well as support back in the office. I am grateful to my Northern Plant Ecology labmates: Carissa Brown, Jayme Viglas, Nicole Wunderlich, Sara Pieper, Kirsten Allen, Xanthe Walker, and Matt Frey for their support and writing critiques; and to Rob Read for a map of Sable Island. Nicole Wunderlich kindly proofread multiple versions of this thesis and gave masterful pep-talks. Digit Guedo provided invaluable statistical brainstorming and coffee breaks.

I further thank Cathy Peters at the W.P. Fraser Herbarium for her help identifying my plants and incorporating them into the permanent collection. I grateful to Allison Muise and David Colville of Applied Geomatics Research Group, Centre of Geographic Sciences, Nova Scotia, who provided distance from shore data and vegetation plot maps. Allison also provided timely encouragement and saved me from many headaches with her beautiful tailor-made maps; I hope to meet her one day. Many thanks to my thoughtful cousin, Alexandre Tissier, for the timely finish work on all maps, as well for responding patiently to my panicked requests.

I thank my mother for encouraging and loving me, as well as for data entry! I also thank my father, step-mother, and sister for constant love and support. My parents instilled in me a great love for nature and curiosity for all things; that passion has shaped all aspects of this project, and indeed, my life. My Alaskan family gave me the skills and confidence to pursue this degree, and continue to support and inspire me. Winton has been my rock over the past 8 years and reminds me to have perspective. I especially want to express my gratitude for Bertrand Charry, who came with me to Saskatoon and supported me through everything. He did an obscene amount of data entry, constantly fueled my heart and mind, and is responsible for immeasurable wonderfulness in my life.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF ABBREVIATIONS

Af: Folded aspect

CART: Classification and regression tree

CV: Cross validation

EW: east – west

GPS: Global positioning unit

HCA: Hierarchical cluster analysis

LiDAR: Light Detection And Ranging

MRPP: Multi-response Permutation Procedures

MFS: Meters from shore

NMDS: Non-metric multidimensional scaling

NS: north – south

SLA: Specific leaf area

1 INTRODUCTION

1.1 ECOSYSTEM DYNAMICS

Coastal dunes are dynamic ecosystems with frequent, often dramatic fluctuations in physical conditions over timescales of hours to days. Energy from waves, currents and winds are typically intense and applied over relatively small areas (Sherman and Bauer 1993). Coastal dunes differ from other coastal land forms in that they are shaped primarily by air rather than water movement. Furthermore, major sand movements on coasts are primarily related to the frequency and duration of extreme winds rather than average wind velocity of a region (Bagnold 1941).

In geomorphology, saltation refers to the bouncing of sand particles picked up by the wind. This process is responsible for 75% of sand movement that leads to dune formation (Pethick 1984). Two other methods of sand transport are surface creep, or the rolling of larger sand particles which never leave the surface; and suspension, where very small particles are suspended in air for varying amounts of time and carried with the wind for distances that are dependent on particle weight and wind velocity. Saltation, combined with the sand trapping properties of vegetation, are what differentiate coastal dunes from desert dune systems, as desert systems generally lack vegetation.

Dune formation in coastal systems begins when sand movement is obstructed. In most cases obstruction is caused either by vegetation or debris, or anthropogenic structures. Any obstruction will slow wind velocity and stop sand movement, generally at the high tide mark where the majority of debris and flotsam are located (Cooper 1967). When sand is deposited, a

dune embryo begins to form (Tansley 1949). These are small and often transient dunes less than one meter high (Bertness 1999). The micro-environmental variability mediated by wind and wave action creates inhospitable conditions for seed germination, emergence of seedlings and their establishment (Maun 1994). Previous studies have shown that on beaches and mobile dunes, seeds can become buried to depths of 20–30 cm (Maun 1981; Maun and Riach 1981). Therefore, burial by sand can have a major impact on seed germination and seedling emergence. In general, the ability of a seedling to emerge depends on the form and weight of the seed and shape of the seedling (van der Valk 1974). Once dunes are colonized, plant roots stabilize the sand against erosion. The above-ground plant biomass promotes further sand accumulation, which traps more seeds and debris, creating a strong feedback between dune growth and plant growth.

Dunes grow until they encounter wind velocities or wave action that limit sand accumulation or erode the embryo. As any dune grows, the point of maximum sand deposition on the leeward face (direction away from the wind) moves closer to the crest (dune summit), causing a steepening of the leeward face relative to the windward face (direction facing the wind). The steepening and growing dune forces wind over the top of the dune rather than down the leeward face. Saltating sand drops out of the air at the crest and further steepens the leeward face until it reaches its angle of repose—about 32 to 34 degrees for dry sand (Bagnold 1941). At that time gravity will pull sand from the crest down the leeward slope. This sand movement is by slippage rather than by saltation or surface creep, and is the reason a leeward face of a dune is also called the slip-face (Bagnold 1941). The slope angle of a sandy surface is very informative regarding the stability of an area. If for example, the surface is greater than the angle of repose,

the surface will be less stable than if the angle is less than 34 degrees. Highly mobile surfaces are less likely to be vegetated.

Embryo dunes typically migrate landwards and, if colonized, merge with other embryo dunes to form a larger, more stable dune called a foredune (Tansley 1949). This is the dune ridge that typically separates transient embryo dunes and more stable, older and larger dunes. As dunes grow in height, they become more vulnerable to the eroding forces of wind until dune height exceeds the binding capabilities of the vegetation. Blowouts are depressions in sand occurring in areas with low levels of binding vegetation cover, either due to a disturbance or low colonization (Tansley 1949). When blowouts occur, the sand is carried a short distance and deposited over existing dune and vegetation formations. Although blowouts start small, they can grow very rapidly with the resulting nearby sand deposits burying existing vegetation communities (E. Tissier, personal observation). Blowouts are common in dune habitats with high wind speed and fast dune growth (Bertness 1999) .

Sand burial of a vegetation community is never uniform. Within a community one portion of the plant population located on the crest or lee of the dune may be completely buried while another part close by may escape the burial event, or it may be destroyed due to erosion. In temperate latitudes, most of the sand accretion or erosion events take place during the fall and winter months when weather is most severe (Harris and Davy 1986).

Nutrient deficiency, lack of moisture, sand erosion and deposition, and moisture stress caused by salt spray are the greatest limiting factors for plants in a coastal dune ecosystem (Maun 1994). Seedlings in these environments employ both avoidance and tolerance strategies to survive stresses. For example, seedlings can rapidly grow roots to reach water and bind sand.

Plant rhizomes also bind sediments (Moreno-Casasola 1988). Sand burial affects plant establishment in foredunes by reducing seed germination, seedling emergence, and survival (Maun 1998).

Below a certain threshold, the growth of all foredune plant species is stimulated by sand deposition because of improved soil resources, increases in soil volume, reactive plant growth, and enhanced mycorrhizal activity as per the "multifactor hypothesis" (Maun 1998). However, as the level of sand deposition and resulting burial increases, the positive response begins to decline until negative responses dominate. At the plant community level, burial acts as a filter by selectively eliminating sensitive species, reducing the relative abundance of less tolerant species, and increasing the abundance of tolerant and sand-dependent species. If sand deposition continues unabated, even the sand-dependent species are eliminated and a bare area is created (Maun 1998). The emergence of a plant after burial primarily depends on the energy reserves in its storage organs and the speed, depth, and frequency of burial. Upon burial the plants shift resources from the below-ground to the above-ground parts. Different plants show varied morphological responses to sand accretion. For example, the culms of grasses respond by increasing the number of nodes per culm and the elongation of internodes. Similarly, the emergent trunks and woody branches of tolerant trees and shrubs produce new buds and suckers at a higher level on the stem (Maun 1998). However, few species can survive complete burial by growing through the sand deposit. Plants respond to salt spray by inhibition of seed germination, increasing leaf thickness, and reducing uptake of Na and Cl ions (Maun 1994).

The strong gradient in physical conditions across dune habitats and the limited ability of plants to deal with various stress factors, leads to plant zonation along different dune zones (Bertness 1999). The zone closest to the water is called the pioneer zone or primary dune

(Tansley 1949) and is characterized by plants with high growth rates and extreme tolerance to dry conditions, high salinity, and sand accretion and erosion. The secondary zone, or dune shrub zone (Tansley 1949), comprises less mobile and less stress tolerant plant species than the pioneer zone such as vines and short woody shrubs. The dune thicket community occurs further from shore than the other two zones and contains short trees stunted by wind and salt spray, and many understory plants found in the dune shrub community (Bertness 1999).

Traditional beach-inland gradients in dune vegetation are well documented (Cooper 1967, Pethick 1984, Lane et al. 2009) and follow a fairly predictable successional trajectory. A temporal and spatial dune succession is often present in coastal dune systems where older and more inland dunes are stabilized beneath increasingly complex vegetation communities and have progressively better developed soils. In general, dune activity decreases with distance from the shore, as do the likelihood of blowouts, resulting in greater dune stability (Salisbury 1952). The typical climax community in these systems is some type of woody shrub or tree community (Bertness 1999).

Forces acting on coastal dunes located on mainland shorelines are different from forces acting on islands. Island dunes are exceptionally dynamic systems where the physical environment, especially storm events, plays a dominant role in shaping biotic communities (Ehrenfeld 1990). As opposed to beach-inland gradients that best capture the dynamics for mainland locations, beach-dune-beach gradients would seem to better describe the interactions for small islands. Even beach-beach gradients where narrow sand dunes are bordered by water may be an appropriate term to capture the environment on small islands especially. Island gradients have not been examined in this framework and may show successional patterns that differ from presenting simply a shortened version of typical beach-inland gradients.

Plant communities on small-island dunes, like those found on Sable Island, Nova Scotia, Canada (my study site), may undergo succession but they are subject to disturbances from all sides, whereas coastal dunes on larger land masses generally experience greatest disturbances from the direction exposed to water. Constant disturbance from many directions, as may be found in small-island systems, makes chronosequence sampling schemes problematic. For example, assumptions that each site studied in a chronosequence differ only in age, and experience similar biotic and abiotic conditions, may not hold true. Critiques of chronosequence methods draw attention to studies in which these assumtions are false (Collins and Adams 1983, Johnson and Miyanishi 2008). If critical assumptions do not apply, using chronosequences to examine change over time will not accurately represent the environment's succession. Instead of examining dune succession through a static chronosequence study, relating the ability of plants to adapt to disturbance might better capture the history of a specific site or area. Observing disturbance-dependent species within vegetation communities and understanding their responses to different disturbances may paint a more intricate picture of the many possible successional trajectories taking place in this dynamic dune system versus a unimodal chronosequence.

1.2 GRAZING AND SAND BURIAL EFFECTS ON VEGETATION

Dune vegetation communities can be vulnerable to animal foraging as well as sand burial (Gedge and Maun 1994). Stresses imposed on coastal dune vegetation from burial and herbivory have many parallels, and my study site, Sable Island, is exposed to both through storm events and grazing or browsing (herein 'grazing') by a feral horse population (see Study Area 2.1).

Vegetation responses to various levels of sand burial may be similar to the compensatory plant growth shown by plants to different levels of herbivory (McNaughton 1983, Gedge and Maun 1994). In this thesis, compensatory growth does not refer to a plant recovering equivalent yield or fitness in response to herbivory; but rather stimulation where plants re-allocate resources away from storage or sexual reproduction and into biomass regrowth. For example, both low to moderate levels of herbivory and partial burial induce reactive growth, increase net CO_2 uptake, enhance dry weight per shoot and seed size, prolong life, and reduce abortion (Gedge and Maun 1994). Herbivory and sand burial have similarly strong impacts at the community level as well. Herbivory alters plant community composition by reducing the abundance of palatable species and increasing the relative abundance of unpalatable species; while sand burial selects for greater survival of sand tolerant species (Daubenmire 1974). Sand movement and herbivory can both pose chronic disturbances to plant communities. Therefore, communities may reach different levels of equilibrium depending on the amount of disturbance present.

Despite some similarities, clear differences between the two types of stress also exist. An herbivore will consume photosynthetic tissue with a complete loss to the plant while sand simply buries the plant parts that remain attached. Some of the biomass and nutrient reserves in the buried parts can be transferred to the aboveground portions of plants (Brown 1997). On a larger community scale, burial will primarily affect plants involved in early phases of primary succession, located in less stable dune areas, while foraging generally disturbs more palatable plants.

Herbivory has been shown to increase dune vegetation and species richness. In Europe, herbivory has been used to restore or conserve coastal dune vegetation communities. For example, in order to stop the continuous decline of dune communities along the Dutch coast,

restoration projects have been carried out since 1952 (Grootjans et al. 2002). These restoration measures consisted of re-introducing traditional management techniques in coastal dune ecosystems, such as mowing, grazing by cows and sod removal (Grootjans et al. 2002). In 1990, grazing was introduced in a section of Meijendel, which is a coastal sand dune system near The Hague, Netherlands. After five years, the total number of plant species in the 19 permanent plots studied, which had been decreasing since 1960, showed a considerable increase with the introduction of horses and cows (de Bonte et al. 1999).

Sable Island's population of feral horses are free to graze throughout the island; however, empirical evidence has yet to be collected suggesting these animals (n = 484 in September 2010, A. Contasti and P. McLoughlin, unpublished data) have either a positive or negative effect on dune vegetation communities. Welsh (1975) theorized that these horses may promote dune destabilization by disturbing vegetation through digging and making trails, leading to an increase in blowouts. However, grazing may have a positive effect via the intermediate disturbance hypothesis (Connell 1978) as suggested by studies in The Netherlands (Grootjans et al. 2002). My project aims to shed light on how plant species on Sable Island respond to different disturbances. Understanding the role of grazing on Sable Island may be especially important for future management strategies aimed at the conservation of biodiversity on the island.

Figuring out the specific ways coastal dunes develop is hampered by the difficulty of measuring and characterizing these processes (Walker 2005, Baas 2007). An alternate approach to understand dune development and vegetation is through the use of airborne Light Detection And Ranging (LiDAR) surveys, which can quickly and accurately map complex dune topography and, through repeated flights, monitor morphological and volumetric changes. LiDAR is yet another tool to get around the difficulties in "on the ground" measurements

(Woolard and Colby 2002). Until recently, morphological coastal studies have been based on a combination of ground surveys of transects and maps or aerial photographs. Ground surveys can provide information about the vertical or horizontal changes at single locations. However any marker or disturbance in sand will result in vegetation change simply by its presence. LiDAR and aerial photos can provide useful information on long-term and short-term advance or retreat of the coast, movement of sediments, and human impacts (Woolard and Colby 2002). Each method has its benefits, for example, it's hard to see the peak of a dune ridge in the aerial photos, but they are clear in the LiDAR. At the same time, the aerial photos are more useful for vegetation mapping. However, several (potentially time-consuming) steps are needed to quantify the rate of change occurring using these traditional methods. The data collected during this study will serve to ground-truth portions of a LiDAR map of Sable Island vegetation by the Applied Geomatics Research Group, Centre of Geographic Sciences, led by Research Scientist David Colville.

1.3 RESEARCH OBJECTIVES

The main objective of my project was to identify relationships between the distribution of plant species, their functional traits, and disturbance severity within the dune ecosystems of Sable Island. I expected that plants with trait adaptations to sand and salt disturbance would increase in abundance as disturbance severity increased, up to a certain disturbance threshold.

In addition to my first objective, I also aim to identify the species/community types that were most grazed on by horses on Sable Island. This may provide an indicator of plant

palatability which may influence habitat selection by the wild horse population. Linking vegetation patterns to dune succession would allow the prediction of how habitat use may change with future disturbance on the island.

2 METHODS

2.1 STUDY AREA

Sable Island, Nova Scotia (43° 56′ N, 60° 00′ W), is approximately 290 km southeast of Halifax (Figure 2.1). The climate is temperate oceanic with cooler summers and milder winters than mainland Nova Scotia. February, the coldest month, has a mean temperature of -1.4 °C; whereas August, the warmest month, has a mean temperature of 17.8 °C (Environment Canada 2010). Prevailing winter winds are south-westerly and average 25.1–31.5 km/h. Summer winds are south-westerly as well and lighter, blowing 17.5–26.2 km/h on average (Environment Canada 2010).

Precipitation on Sable Island averages 146 cm/yr and is unevenly distributed throughout the year. December and January are the wettest months, averaging 14.7 cm/month; the driest month is July, averaging 9.2 cm (Environment Canada 2010). Nine percent of the annual precipitation is snowfall. Because the island is in the path of storms year-round as well as hurricanes and tropical storms in the summer and fall, most of its precipitation comes from large-scale storms. Thunderstorms are infrequent, but hurricanes and tropical storms bring heavy rain to the island. The highest hourly wind speed observed is 130 km/h, with gusts reaching 174 km/h

(Environment Canada 2010), or even to 190 km/h. On average, 127 days a year have at least one hour of fog. July has 22 fog days on average and is the foggiest month (Environment Canada 2010).

Sable Island is crescent-shaped and entirely composed of sand and roughly 40 km long and 1.5 km across at its widest point (Figure 2.2). The tips of the island terminate as sand bars that seasonally fluctuate in size. Sable Island is the only emergent portion of the outer continental shelf in the Atlantic Ocean (Cameron 1965). Specifically, it is the peak of Sable Island Bank which is part of a series of banks located on the outer region of the Scotian Shelf (James and Stanley 1968). Sable Island was formed during the retreat of the last glaciation and is currently held in place by the southwardly flowing Labrador Current, and the northeastwardly flowing Gulf Stream. These currents together with prevailing winds continue to shape the island's physiography (James and Stanley 1967).

Sable Island's north beach and south beach are bordered by a row of sand dunes that average 9 to 12 meters high, with a maximum elevation of 25 meters towards the eastern end (Byrne and McCann 1993) . Dune blowouts are widespread along both sides of the island and can range up to 10 meters deep and 30 meters across (personal observation). The interior topography is characterized by low rolling dunes with numerous freshwater ponds, especially in the western half of the island.

Since 1505, Sable Island has been described as treeless (save one individual of *Pinus sylvestris*) , sandy, and vegetated by low growing forbs, grasses and shrubs (Gilpin 1858). Preparations to colonize Sable Island began in 1518, when the Baron de Lery released horses, cattle and rabbits to be used in future settlement (Elstracke 1625). In 1598, Troilus de Mesgouez,

Marquis de la Roche, settled the island with fifty French convicts and ten soldiers. They established a garden but largely survived on seals, fish, and the descendents of the animals released 80 years earlier. Five years later the men were rescued by Captain Thomas Chefdostel, who found only twelve of the original sixty alive. Eventually, the island's livestock were harvested by American and Acadian colonists, and by 1668 no livestock were on the island (Catling et al. 1984). No more settlements were made during the 1600s, though a few unsuccessful attempts were made in the 1700s. Some livestock, including horses, sheep, cows, and pigs, were reintroduced when Father Andrew LeMercier colonized the island in 1738 (LeMercier 1753). It is theorized that some of LeMercier's horses are the ancestors of the herd that presently inhabits Sable Island; other historians believe that the present herd are descendents of individuals placed on the island by Thomas Hancock around 1760 (Christie 1995). Horses are presently the only terrestrial mammal on Sable (other than humans).

The Experimental Farm in Ottawa initiated a large-scale planting project on Sable Island in 1901. This initiative included the introduction of over 80,000 trees to the island, including, "68,755 evergreens of 25 varieties, and 12,590 deciduous sorts of 79 varieties … as well as 50 pounds of the seed of the Maritime Pine, *Pinus maritima*" (St. John 1921). By 1913, only 77 of the original plantings had survived (St. John 1921), and by 1952, only one individual of Alder Buckthorn *(Frangula alnus)* remained (Erskine 1953). This effort to introduce non-native species on Sable Island was unsuccessful, implying that only plants adapted to its set of extreme environmental conditions will survive. Many studies have examined the plants of Sable Island, (Gilpin 1858, Macoun 1900, St. John 1921, Erskine 1953, Keddy 1975, Catling et al. 1984, Stalter and Lamont 2006) however, none have examined their distribution along disturbance gradients.

Human impacts on Sable have left a legacy of ecological disturbance. Known as “The Graveyard of the Atlantic”, Sable Island is the site of over 350 recorded shipwrecks since 1538 (Campbell 1994). Several reasons account for this staggering number. The currents around Sable are complex as it lies at the junction of the Gulf Stream and the Labrador Current. Its location near one of the world's richest fishing grounds has drawn many vessels to the area. It is also in the path of major shipping routes between Europe and North America (Campbell 1994). Due to its propensity for shipwrecks, the colonial government of Nova Scotia established a permanent life-saving station in 1801 (Stilwell 2001). Two lighthouses, one on the eastern tip and one on the western tip, were built in 1872 (Irwin 2003). Since then, there has been a continuous presence on the island including staff and family of lifesaving communities, shipwreck victims, lighthouse keepers, sealers, oil drillers, meteorological staff, scientists, and a few tourists.

2.2 SAMPLE DESIGN

I sampled the vegetation of Sable Island from 16 July to 2 September 2010 using a stratified random sampling design. The island was separated into eight sampling longitudinal sections of varying size based on concurrent studies of horse habitat use and distribution on the island. These sections previously had been determined based on topographic variability and vegetation cover area. Three longitude lines were randomly selected within each of the eight sections and were used as the start of all 24 north/south running transects (Figure 2.3A).

To capture similar temporal variance in all sections, only one transect was sampled for a section per day. The following day, another section was selected so that all sections were

sampled relatively evenly throughout the sampling period. To ensure sample plots were capturing the full spectrum of the north/south shore gradient each transect was divided into zones based on their distance from north or south shore: near shore (0–100 m from shore), far shore (100–250 m), and center zones (>250 m). Zone length ranged from 100 to 299 m. If a center zone was less than 100 m long it was incorporated into the nearest center zone (Figure 2.3B).

Zones were used to stratify sample plots with a fixed sampling intensity of one plot per zone. The start of each transect was the water's edge at the chosen longitudes. To determine where a plot would be located within a zone, a random number was chosen as the distance to walk from the zone's perimeter. This distance was measured with a GPS while direction was measured with a compass as either due north or south depending on which shore was the starting point of the transect. One plot was placed in each zone of each transect totaling 135 plots for the whole island. A center stake was placed one meter to the right of the transect at the selected distance to mark the center point of each plot to avoid the area disturbed by walking the transect.

To set up each plot, a compass was used to determine the four cardinal directions from the center point. Four additional stakes were placed 2 m from the center point at the four directions. Four 0.5 m^2 quadrats were placed within each 2 m circle, one along each line between the center stake and cardinal direction stakes. Distances from the center stake were randomly chosen as either 0 m, 0.5 m, 1.0 m, or 1.5 m. Each quadrat was placed to the right of the line between the center stake and the cardinal direction center stake. Each 0.5 m^2 quadrat was divided into four equal subsections (Figure 2.3C).

2.3 FIELD MEASUREMENTS

A waypoint was taken at the center point of the plot and coordinates were recorded, along with elevation (m) from the GPS and plot number. Slope (degrees) was measured using an inclinometer and aspect (degrees) with a compass. Topographical plot position was recorded as one of ten possible categories: crest, shoulder, side slope, toe slope, valley bottom, wet inter dune slack, depression, freshwater pond, blowout, or beach. The site contour was visually estimated as either: flat, convex, concave, or undulating.

All vascular species present within the 2 m circle were recorded and indentified according to Manual of Vascular Plants of Northeastern United States and Adjacent Canada (Gleason and Cronquist 1991). A voucher specimen was collected for plant species that could not be positively identified in the field to verify correct identification.

Several observations were collected in each plot. Each species within the 0.5 m^2 quadrats was given a score of 0 to 4 according its presence or absence within the four subsections of the quadrat (Appendix A.1 and A.2). If a species was present in the 2 m circle but not in any of the four plots, it received a score of zero. Therefore, 0 was the minimum score possible and 16 the maximum score. Presence/absence was used to measure the relative abundance of each species as this method is less influenced than cover assessment by observer bias (Critchley and Poulton 1998) and reduces time spent at each plot. Organic layer presence or absence was measured by excavating soil with a trowel at each plot center point (Appendix B.1). Evidence of human disturbance, horse trails, or animal carcasses was also recorded where encountered. Other general observations describing any unique attributes were noted and a photo was taken of each

plot (Figure 2.4). If erosion occurred, the maximum root distance above ground was measured to the nearest cm and recorded for each quadrat. I scored evidence of grazing on a scale of 0 to 4 (0 = no evidence of activity, 4 = abundant evidence of activity in all quadrats of a plot) for each plot as I did with plant species abundances (Appendix C.1).

Measurements of plant traits were not made at each sampling plot, rather five individuals of each plant species observed in this study were randomly chosen and their heights measured. One leaf from five individuals of each plant species were randomly chosen and pressed in a plant press for use in determining specific leaf area (SLA). All leaves of succulent species were traced when harvested in order to capture a more accurate representation of fresh leaf area. Because of its applicability across different floras, SLA appears to be the best candidate to compare growth strategies for large databases (Vendramini et al. 2002). Other plant traits were also noted: presence of waxy or succulent leaves, presence of creeping or fibrous roots, ramet type (clumped, spreading, or dispersed), perennial, and Raunkiaer plant life form (Appendix C.1). Plant traits that were not measured in the field were taken from Manual of Vascular Plants of Northeastern United States and Adjacent Canada (Gleason and Cronquist 1991).

2.4 LAB MEASUREMENTS

I measured the area of five leaves of each species using a flat-bed scanner and Win FOLIA software (Regent Instruments Inc, Ste-Foy, Quebec, Canada). The exception was *Sisyrinchium angustifolium* P. Mill., whose leaves were unable to be collected in August, and were therefore not included in SLA analysis. Even though leaves, petioles, and stems are different organs,

following Westoby (1998) I considered all structures that are shed at abscission as part of the leaf. For practical purposes I considered a 'leaf' as the structure that carries out most of the photosynthesis. Therefore, SLA analysis applies to photosynthetic stems, etc., as well as to true leaves (Vendramini et al. 2002). The entire plant was considered a leaf for *Juncus arcticus* var. *balticus* (Willd.) Trautv., as well as *Spergularia salina* J. & K. Presl; therefore the entire plant was scanned. Where species had compound leaves with leaflets overlapping, the leaflets were removed from the petiole and scanned after separation. Next, all scanned leaves were dried at 30˚C for four days and weighed at room temperature. SLA was calculated from these values as leaf area cm^2 divided by grams of that leaf. Very small samples were pooled and all five leaves weighed together to increase accuracy.

Measurement accuracy for small leaves like *Calluna vulgaris* in particular could be improved by weighing several leaves together (Cornelissen et al. 2003), which was the method I used for all small-leaved species. Additional challenges to obtaining accurate measurements were due to logistical constraints. Although it is recommended that leaves be scanned fully hydrated and within 48 hours of collection (Cornelissen et al. 2003), this was impossible because no equipment was available on the island and no resupply flights were available to transport materials. I traced each succulent leaf to capture a more accurate fresh leaf area, rather than a dehydrated sample that was in the plant press for several weeks. Unfortunately, I do not know how important the different variations in potential error were. By grouping species that had SLA values in a similar range, the exact SLA value was less important and could be represented by a range of values. Future research that aims to link specific values for different plant traits would benefit from following the protocol in Corneilssen *et al.* (2003) and obtaining a leaf scan of fully hydrated leaves and a larger sample size.

All plants that were not able to be identified in the field were brought to the W.P. Fraser Herbarium at the University of Saskatchewan. There, the samples were identified using the Manual of Vascular Plants of Northeastern United States and Adjacent Canada (Gleason and Cronquist 1991) as well as herbarium specimens for comparison. All collections were donated to the W.P. Fraser Herbarium at the University of Saskatchewan.

Several different ways of assessing aspect were tried. Folded aspects (*Af.*) along the north-south (*NS*) line were calculated as:

$$Af.NS = 180 - |aspect - 180|$$

Folded aspects along the east-west (*EW*) line were calculated as:

$$Af.EW = Af.NS + 90$$

Aspects that had no values because zero slopes were changed to the mean value of each folded aspect. A simplified method of analyzing plot orientation was devised and used as north facing = 1, flat = 0, and south facing = -1.

2.5 DATA ANALYSIS

2.5.1 VEGETATION DISTRIBUTION

In order to investigate patterns in the distribution and abundance of plant species across the island I investigated the distribution of each species across different measured environmental gradients. The total abundance of each plant species was calculated by summing the number of quadrats where each species was present across all 134 plots.

2.5.2 *CLASSIFICATION AND REGRESSION TREES*

Classification and regression tree (CART) analysis is a non-parametric method that partitions a data set into increasingly homogeneous subsets, identifies and estimates the interactions of predictor variables, and represents them in a relatively simple form (De'ath and Fabricius 2000). CART analysis is robust to non-linear relationships among variables as well as combinations of ordinal and continuous variables. I used a univariate CART analysis to determine the most important factors influencing whether a plot was vegetated or not. All 134 plots were used in this analysis with a Boolean response variable of 1 for plots with vegetation present, or 0 for unvegetated plots. Predictor variables were environmental variables measured in each plot. I used the package "rpart" (Therneau et al. 2010a) in R (R Core Development Team 2010).

I also used CART analysis to discover the most important factors affecting levels of grazing evidence (0–4). Using data from vegetated plots (n = 67), predictor variables were: abundance levels (0–16) for the six most common species, orientation, slope, elevation, distance from south shore, distance from north shore, and presence of an organic layer.

2.5.3 *HIERARCHICAL CLUSTER ANALYSIS*

A hierarchical cluster analysis (HCA) was used to detect groups of plots in my sample that shared similar patterns of species composition (McCune and Grace 2002). Plots were clustered using the "cluster" package (Maechler et al. 2005) in R based on species abundance values using Ward's method of minimum variance linkage (Ward 1963). Ward's method minimizes the increase in the sum of squares error (distance from individual to centroid of group) as plots are

aggregated. This method assumes that a cluster is represented by its centroid, and measures the proximity between two clusters in terms of the increase in the sum of squares error that results from merging the two clusters (Ward 1963). I used a Euclidean distance measure for this analysis because Bray-Curtis (Sørensen quantitative index) is incompatible with Ward's method (McCune and Grace 2002). To assess the most appropriate number of clusters, I plotted the within-groups sum of squares (Ward's variance) against the number of possible groups for the dataset. The best number of groups was selected as the number associated with reduction in the change in slope of (i.e. an elbow in the scree plot), such that the sums of squares would not greatly decrease by adding another cluster (McCune and Grace 2002). Chaining, the sequential addition of single plots or small groups to larger groups, was calculated as a percentage by comparing the average path length of the dendrogram with the minimum and maximum possible path lengths (McCune and Grace 2002). Path length is the number of nodes between the base node and terminal node for each plot. Because approximately half of the sampled plots were unvegetated I split the data and focused the analysis on plots that had two or more species present after removing rare species that were observed in only one study plot.

2.5.4 MULTI-RESPONSE PERMUTATION PROCEDURES

Multi-response permutation procedures (MRPP) were conducted using PC-ORD (McCune and Mefford 2011) to test the difference between different vegetation groups found with HCA (Mielke et al. 1981, Zimmerman et al. 1985). Additional MRPP were conducted for the two subgroups found within group 1 of HCA. MRPP is a non-parametric test that determines the difference between two or more *a priori* groups (McCune and Grace 2002). The dataset used for

MRPP was the same for HCA. Both Euclidean and Bray-Curtis distances were used to conduct separate MRPP because these distances were used for both HCA and ordination techniques, respectively. Chance-corrected within-group agreement (*A*) was determined. *A* values of 1 indicate all items within groups are identical, whereas values closer to 0 represent heterogeneity within groups equal to that expected by chance. Statistical significance, *p* values, are also given for each MRPP run. I recognize that tests of group distances were based on the same data that were used to define the groups, therefore probability levels do not represent an independent test of significant differences among groups.

2.5.5 INDICATOR SPECIES ANALYSIS

I used indicator species analysis (Dufrêne and Legendre 1997) to determine which plant species were indicators of each three main *a priori* groups determined by HCA, as well as the two subgroups that comprise group 1. An indicator species has a high indicator value (*IV*) and low probability ($p < 0.05$) of obtaining an *IV* of equal of higher value by chance (McCune and Grace 2002). Significant indicator species are species highly characteristic of that *a priori* group, whereas a perfect indicator of a group is one that is always present and exclusive to that group (Dufrêne and Legendre 1997). The *IV*s for a species was calculated by taking relative abundance and frequency of each species in each group, and used randomizations to identify significant indicator species. Indicator values (*IV*) were tested for significance using 1000 permutations of a Monte Carlo test (Metropolis and Ulam 1949) in PC-ORD.

2.5.6 ORDINATION ANALYSIS

I performed an ordination analysis of vegetation composition using non-metric multidimensional scaling (NMDS) in the "MASS" package (Venables and Ripley 2002) in R to ordinate my sites in species space. NMDS uses rank distances which tend to linearize the relationship between the distances in species and environmental space, reducing the "zero-truncation problem" common to many ecological datasets (McCune and Grace 2002). NMDS avoids assumptions of normality and linear relationships among variables, and produces interpretable results when analyzing ecological data (McCune and Grace 2002). Because my data were ordinal, a ranked-based (ordinal) analysis is the most compatible (Podani 2005). NMDS is an iterative process and produces a solution of sample plot positions in species space with the lowest stress. Because of this iterative process, multiple runs with random starts are necessary to avoid local minima (McCune and Grace 2002). I chose the most appropriate number of dimensions for the NMDS based on a scree plot showing stress in relation to dimensionality (McCune and Grace 2002). I created a stress plot to assess the non-metric and linear fit of the ordination distances with observed dissimilarities. I selected the Bray-Curtis distance measure to calculate my dissimilarity matrix because it has been shown to be effective for ecological data and is compatible with ordinal data (McCune and Grace 2002). Ordinations were run on species abundance in plots (range of 0–16). I used vector overlays to determine to what extent the abiotic variables might influence species distribution, as well as which variables are most strongly correlated to certain plots.

A common attribute of ecological data, especially along severe environmental gradients, is the presence of empty samples. When enough is known about the data to say the samples may

be empty, or nearly so, from the same cause rather than by random occurrences, it may be more meaningful to modify the dissimilarity measure to force it to return the value 0 rather than remain undefined (Clarke et al. 2006). Although I attempted to use this analysis approach by using a 'zero-adjusted' Bray-Curtis in my NMDS ordination, I was unable to obtain a stable result because over half of my full dataset consisted of unvegetated plots. Consequently, I conducted a second NMDS ordination analysis using all species observed (n = 33) and only vegetated plots (n = 67). This analysis was unable to produce meaningful results (very high stress) due to high β-diversity or turnover of species among plots. To reduce species turnover associated with the presence of rare species or sparsely vegetated plots, I reduced the species used in the final NMDS ordination to those that occurred in at least two study plots (n = 24), and only included plots that had two or more species present (n = 44).

Vector overlays were used to assess the relationships between measured environmental variables or plant traits with patterns of plant community composition. Vector overlays were calculated using the *envfit* function in the "vegan" package (Oksanen et al. 2011) of R. The angle of each vector is represented by a hypotenuse for each variable where the other two sides are r^2 values of the variables and each axis. The length of each vector represents the strength of the relationship between the vector and each axis. Environmental variables used as vector overlays were: organic depth (cm), grazing evidence, site contour, elevation (m), slope (˚), plot position, and distances from the north and south shores (m). Relative abundance of plant traits were also used as vector overlays on the final NMDS to determine if certain plant assemblages shared similar traits. Relative abundance weighted values for traits were calculated by summing the number of plots where the trait occurred and dividing it by the total number of observed

vegetated plots. Continuous variables, height and SLA, were arbitrarily grouped into classes of similar values.

2.5.7 MULTIVARIATE REGRESSION TREES

I ran a multivariate regression tree (MRT) analysis (De'ath and Fabricius 2000, De'ath 2002) to investigate what environmental factors most influenced the distribution of the 6 most abundant species on Sable Island: *Achillea millefolium* L., *Ammophila breviligulata* Fern., *Festuca rubra* L., *Lathyrus japonicus* var. *maritimus* (L.) Kartesz & Gandhi, *Poa.*spp, *and Rosa virginiana* P. Mill., using data from every plot vegetated with these six species (n = 61). MRT models partition the data recursively into subsets that are increasingly homogenous just as classification and univariate regression trees do, but using multiple predictor and multiple response variables. The result is a hierarchal tree in which different groupings of habitats are identified as different branches of the dendrogram. The solution identifies the variables associated with each branch, while also providing a dichotomous tree that can classify new samples accordingly (McCune and Grace 2002, De'ath 2007). Because MRT uses a recursive process and can predict multiple responses, it is used most often to classify habitats of vegetation types determined by environmental conditions (De'ath 2002) . Based on the cluster size with smallest mean SE (De'ath 2002), I pruned the tree to the most meaningful grouping size, using the mvpart package (Therneau et al. 2010b) in R. The pruning is determined by cross-validation (CV) using a cost-complexity function that balances the apparent error rate with the tree size (De'ath 2002). A by-product of this procedure is a CV estimate of the error rate.

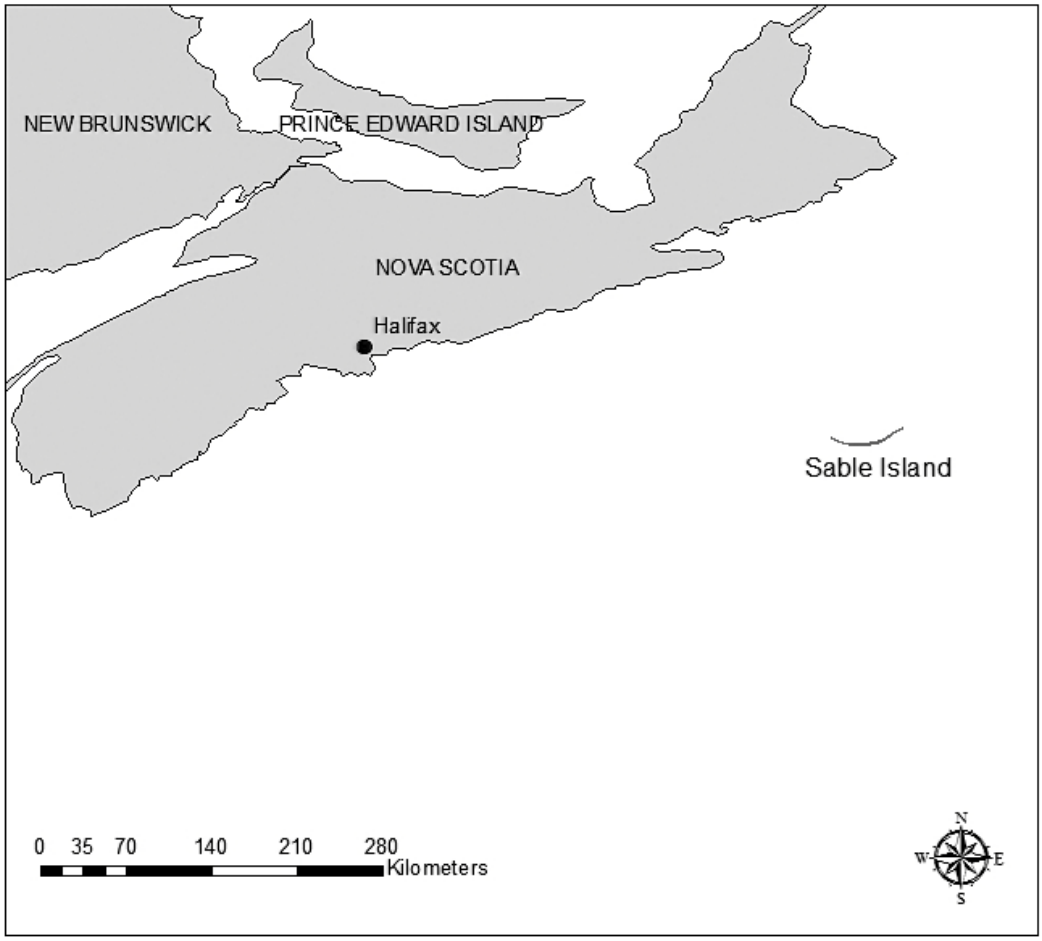

Figure 2.1: Map to show position of Sable Island, Nova Scotia, relative to mainland. Map produced in ArcGIS by Rob Read at the University of Saskatchewan.

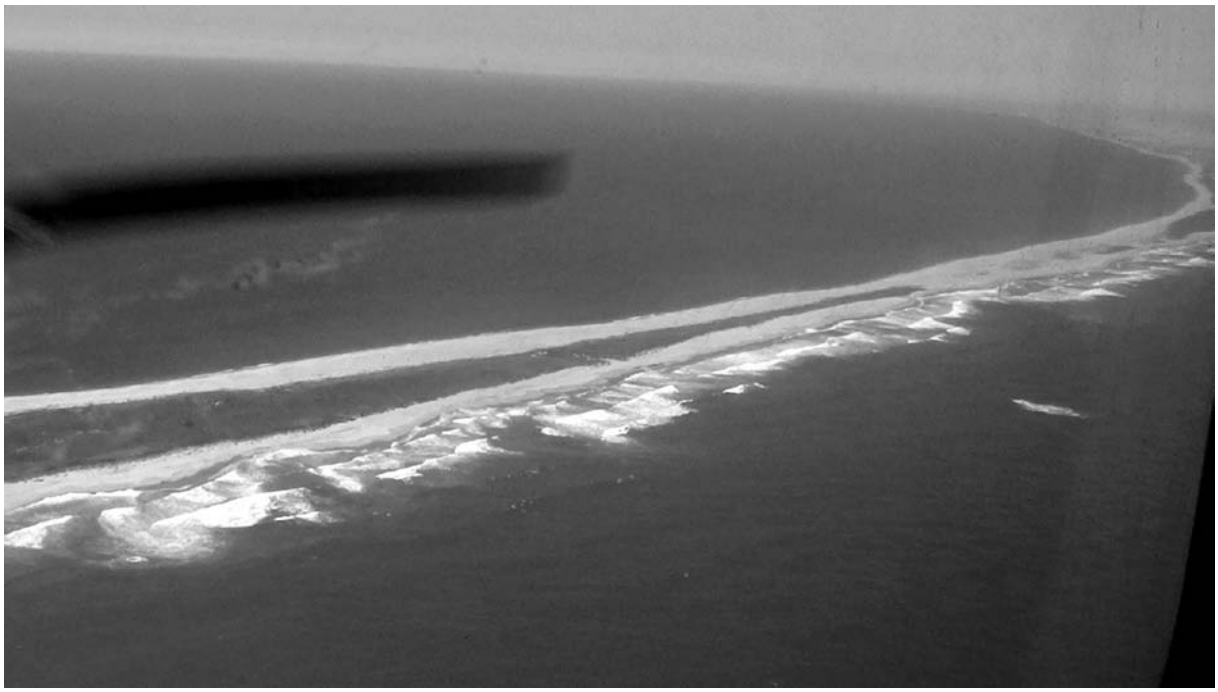

Figure 2.2: Photo of Sable Island's west tip on aerial approach by Emily Tissier 2010.

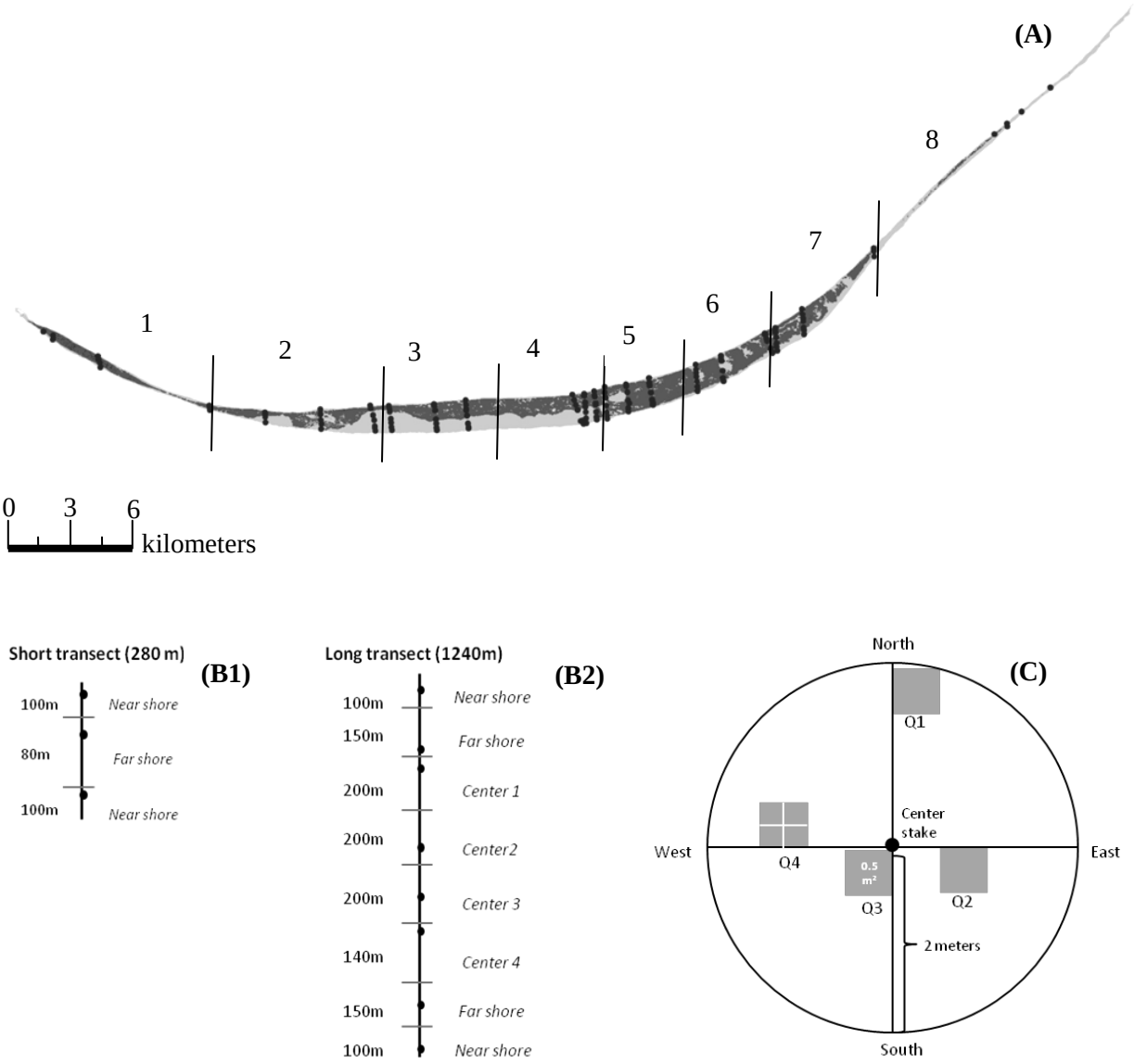

Figure 2.3: Schematic diagram illustrating the stratified random design used for sampling vegetation on Sable Island. **A)** Sable Island with eight sampling sections separated by black lines and labeled with each section number above the corresponding section. Black dots represent sample plot locations along at least 3 north – south transects per section. Map created by Allison Muise of Applied Geomatics Research Group (AGRG) and Alexandre Tissier. **B)** Short (B1) and long (B2) transect examples with associated zones of distance from shore. One plot (black dot) is located within each zone. Zone lengths are to the left of the transect and zone names are written on the right of transect lines. **C)** Scheme of each individual plot. 2 m^2 circle with north – south and east – west cross-sections, gray squares are 4 quadrats located within each plot. White lines within one quadrat represent four subquadrats (in each of the four subquadrats). The black dot represents the center of the plot.

Figure 2.4: Photo of a vegetation plot with one center stake and 4 corner stakes with flags attached. The white cooler contained vegetation samples. Photo by Emily Tissier 2010.

3 RESULTS

I sampled 134 plots within eight east-west sampling blocks on Sable Island that spanned the entirety of the island (Figure 2.4 A). Of these plots, 67 had no vegetation present and 67 had at least some vegetation present. Of the vegetated plots, 21 plots had only one species present, 11 plots had two species, 8 plots had three species recorded and 27 plots had four or more species present. *Ammophila breviligulata, Lathyrus japonicus* var. *maritimus, Festuca rubra, Achillea millefolium, Poa* spp., and *Rosa virginiana,* were most common species with the highest summed total abundance (Table 3.1). I examined levels of grazing in vegetated plots for all species combined and found island sections three, six and eight to have the lowest median recorded levels (Figure 3.1).

Regression tree analysis indicated that the majority of plots with vegetation were found in areas with a slope between 1.5˚and 26.5˚and at distances greater than 39.5 m away from shore (Figure 3.2). Unvegetated areas tended to be completely flat because their lack of vegetation meant there was nothing to stop sand movement and accumulate sand, and hence no initiation of dune formation. These areas were also commonly found near the shore at distances of <39.5 m, where frequent erosion, sand accretion and tidal over-wash also hindered dune formation. Steeply sloping plots likely experienced frequent sand movement because the angle of repose for sand ranges from 15˚ to 35˚ for dry and water-filled sand respectively (Bagnold 1941). I pruned the tree to 4 terminal nodes as this number yielded the lowest cross validation error (Figure 3.3). When analyzed separately, distances from north and south shores produced branching events in

the tree at thresholds of 39.5 and 38.5 meters respectively, therefore total distance to either N or S shore was used to simplify the tree.

A second CART analysis indicated that the majority of grazing evidence occurred between the slopes of 0.5˚and 17.5˚(Figure 3.4). None of the plots on slopes steeper than 17.5˚ (n = 3) had evidence of grazing and only one plot with a slope of less than 0.5˚was grazed on. Although vegetation occurs at steeper slopes than 17.5˚, horses seem to prefer grazing or browsing on flatter slopes that are more stable. Because angle of repose is so variable, slopes that sustain horse movement might fall below the 17.5˚threshold. The lowest cross-validation error for the grazing CART analysis occurred at three nodes (Figure 3.5). Despite all six most common species and multiple environmental variables being included in predictor variables for this CART analysis, slope was the only variable used in the classification tree. Other CART analyses to assess evidence of grazing were conducted using a combination of all environmental variables combined with abundance data for every species collected, and alternatively only environmental variables; the results of these preliminary analysis showed the same trend in slope thresholds being the most influential variables to predict occurrence of grazing.

A hierarchical cluster analysis (HCA) identified three different groups of plots based on their vegetation composition. This analysis used only plots vegetated with two or more species, and data for species occurring in at least two or more plots (44 plots × 24 species). Based on an analysis of within-group sum of squares versus possible total cluster numbers, a group size of three was the most appropriate number for the HCA. The HCA grouped plots based on vegetation community composition and abundance in each plot (Figure 3.6). Each of the groups was separated by a long stem in the diagram, indicating a “natural” grouping (McCune and Grace 2002). The final cluster analysis had an agglomerative coefficient of 0.866. Agglomerative

coefficients near 1 indicate a very clear structure has been found in the cluster analysis. In addition, this analysis had 5.86% chaining which indicated a relatively low path length, or proportion of only single items added to an existing group.

In community ecology MRPP values for *A* (chance-corrected within-group agreement) are often lower than 0.1 and values greater than 0.3 are considered high , and hence of greater value (McCune and Mefford 2011). MRPP results for the three groups determined by HCA indicate they are significantly different from each other ($A = 0.25$ for Euclidean, and $A = 0.28$ for Bray-Curtis, $p < 0.001$ for both distance measures). Results for two subgroups within group 1 were also significantly different from each other ($A = 0.16$ for Euclidean, and $A = 0.15$ for Bray-Curtis, $p < 0.001$ for both distance measures). The groups found by HCA appear distinct.

My indicator species analysis results identified three indicator species for group 2, and ten indicator species, of which six were perfect indicators, for group 3 (Table 3.2). These species are indicators of each group because they were found at higher frequencies and abundance in that group than any other group. There were no indicator species for group 1, however when the two subgroups were examined exclusively, *Honckenya peploides* ($IV = 44.7$, $p = 0.028$) and *Lathyrus japonicus* ($IV = 75.3$, $p = 0.001$) were significant for subgroup A, whereas *Festuca rubra* ($IV = 46.2$, $p = 0.014$) was significant for subgroup B.

Separation of the three main groups in the HCA dendrogram (Figure 3.6) was largely related to stress exposure as represented by gradients in distance from shore and slope. Group 1 represented plots located in areas of high disturbance, group 2 plots occurred in locations with moderate environmental stress, and group 3 plots were farthest from shore and likely had the lowest levels of environmental stress.

Patterns in vegetation composition were also explored with ordination analysis using NMDS. Initial assessment of stress versus dimensionality indicated that a two-dimensional solution showed the greatest reduction in stress, while addition of further dimensions to the solution had relatively small effects on stress (Figure 3.7). The final two-dimensional NMDS ordination used 50 random start iterations and yielded a stress of 12.32. NMDS ordinations maximize rank-order correlation between distance measures and distance in ordination space. The closer the points fall to the monotonic line of a perfect relationship between the dissimilarity measure and ordination measure, the lower the stress (McCune and Grace 2002). Each site's location in the ordination (Figure 3.8) provides information on the relative similarity of vegetation composition between plots. Plots located closer to each other are more similar than plots located far apart. This ordination showed that groups of plots identified in the HCA occupied relatively distinct regions of space in the ordination. The common pattern of plot clustering in both analyses confirms that these 3 different vegetation community types group similarly regardless of the analysis approach.

My statistical analysis using ordination presented several limitations to a more complete understanding of the vegetation communities on Sable Island. A large constraint was omitting mono-culture plots for the ordination analysis, which represent 21 of 67 vegetated plots sampled. These plots were largely vegetated by either *Ammophila breviligulata* or *Honckenya peploides*, two of the most widespread species on the island which accounted for a large part of vegetated area. I suspect the plots with mono-cultures of these two species represent environments with either very high sand disturbance and/or salt spray as these two species would out compete other less well adapted species in these circumstances. When considering the gradient of

environmental stress from shore, these mono-culture plots most likely represent the early pioneer communities responsible for initial establishment and dune development.

Another limitation of the ordination analysis was omitting species that were observed only once. How to handle rare species in a statistical analysis is a common problem for ecologists (Welsh et al. 1996). The exclusion of rare species typically contributes little to interpretive value and adds noise to the statistical solution. Most importantly, the removal of these species in this study allowed the distance matrices to be calculated because it is impossible to calculate a dissimilarity value with only one data point. Although these species accounted for only a very small portion of observations, it is still a loss of all associated data such as trait and environmental variables. Had there been a larger sample size or large plot size, some rare species might have been captured more often. Regression tree analysis did, however, include all plots which captured the thresholds at which these omitted mono-culture plots existed. The combination of several analyses allowed for weaknesses in some methods to be compensated for by others.

Correlations of ordination axes with environmental variables provided a means to explore the underlying environmental gradients that may be shaping the distribution of plant communities on Sable Island. The strongest correlations with environmental variables were with the presence of organic layer, meters from north shore, presence of grazing, and meters from south shore (Table 3.3). Vector overlays illustrate group 1 plots were associated with locations closer to the south shore, group 2 plots were associated with the presence of an organic layer, and group 3 plots were associated with locations nearer the north shore (Figure 3.8). Both groups 1 and 2 were related to presence of grazing. Presence of an organic layer was negatively correlated with distance to the south shore. Presence of an organic layer is found inland where

vegetation is less disturbed. Note also that group 2 plots form the tightest cluster, a trend also evident in the classification (Figure 3.6). Based on these environmental correlations, it appears that the communities represented by group 1 are tolerant of high environmental stress, whereas group 2 tolerates moderate levels of environmental stress. Group 3 tolerates the lowest levels of environmental stress on Sable Island.

An NMDS ordination plot showing species centroids illustrates that plots in group 1 supported high cover values of species such as *Ammophila breviligulata* and *Honckenya peploides*, which can tolerate high levels of sand and salt disturbance (Maun and Lapierre 1984, Gagné and Houle 2002) (Figure 3.9). Group 2 plots were composed of vegetation that tolerates disturbance moderately well such as *Achillea millefolium*, *Lathyrus japonicus*, *Rosa virginiana* and *Maianthemum stellatum* (L.). Group 3 plots were populated by the least disturbed communities of shrub-heath. Typical species in group 3 plots are *Empetrum nigrum* (L.), *Myrica pensylvanica* (Mirbel), and juniper whose stress tolerance characteristics include reduction of water loss by waxy leaf surfaces and woody stems.

Examining plant traits as vectors for the NMDS showed which traits were most common for each vegetation group. Three Raunkiaer plant forms (Raunkiær 1905) and all height classes (Table 3.4) are illustrated as vectors (Figure 3.10) because they had the strongest correlation coefficients with Axis 1 and Axis 2 of the NMDS ordination. Group 1 was most strongly correlated with tall plants and hemicryptophyte life forms which are plants with buds situated at or just below the soil surface. Hemicryptophytes are usually herbaceous perennials. Geophytes, plants with an underground storage organ, were most commonly associated with group 2, which also had highest correlations with spreading ramets, waxy or succulent leaves, and the highest SLA values recorded on Sable Island ranging from 164 to 228 (Table 3.4). Traits most associated

with group 3 were short to medium plant heights and chamaephytes; low-growing plants whose buds are either at or near (within 0.25 m of) the soil surface. Chamaephytes typically include small bushes and herbaceous perennials typical of group 3 species. Group 3 was also correlated with SLA values ranging from 30 to 65 (the lowest values recorded on Sable) and 134 to 148 (a mid-high range for species on Sable). *Moehringia lateriflora* (L.) Fenzl, was excluded from SLA analysis as it had an extreme value of 1495 due to unknown measurement errors.

Several factors contributed to the difficulties of obtaining accurate SLA measurements. Some plant formations make an accurate measurement of surface area by scanning the leaves impossible. For example, many species had bipinnate and tripinnate leaves or leaves that are not completely flat with crisped margins, such as *Achillea millefolium* and *Rumex crispus*. In addition, folded leaves from *Festuca rubra* and overlapping leaflets in *Thalictrum pubescens* also posed a problem as to whether you choose to flatten the folded leaf and pluck apart the leaflets to scan the area separately or not. *Juncus* spp. were tricky to compare to other species because the entire upper plant part was scanned as the leaf. Finally, plants with needle-like leaves such as *Empetrum nigrum*, and junipers posed a problem because these leaves were thick and had a greater surface area than a scan could capture.

Multivariate regression tree analysis of environmental factors affecting the distribution of the six most abundant species on Sable Island indicated that a tree with 4 terminal nodes had the lowest cross-validated relative error (Figure 3.11). Results of the 4-node regression tree analysis suggest that the distribution of these common species were most strongly influenced by the environmental gradients of distance from south shore, organic layer depth, and distance from north shore (Figure 3.12). The pruned tree indicates that *Ammophila breviligulata* dominates the communities with less than 0.5 cm organic depth regardless of distance from north shore.

Organic layers were not found in areas of high sand deposition which is the environment *Ammophila breviligulata* thrives in. Plots found less than 115.5 m from the south shore had higher abundances of *Achillea millefolium, Ammophila breviligulata, Lathyrus japonicus,* and *Poa* spp., while *Festuca rubra* was noticeably absent from those plots. Plots further than 115 m from the south shore and with an organic layer greater than 0.5 cm thick had the highest abundances of *Festuca rubra* and *Rosa virginiana*.

Table 3.1 (following page): Species list of all species observed in plots for this study organized by family name, genus, and species, along with a summary of leaf traits ($n = 5/species$) and percent occupancy (n = 134 plots, n = 2144 sub-quadrats). Mean leaf area is given in cm^2. Mean weight was calculated by weighing all 5 leaves together and dividing by 5. Specific leaf area was calculated by dividing the cm^2 leaf area by the leaf weight (g). Values of 2 m^2 represent whether the plant was present or absent within the entire plot, while quadrat values represent the total number of quadrats containing each species across all plots.

	Mean leaf area (cm^2)	Mean leaf weight (g)	SLA** (cm^2/g)	species occupancy			
				All plots (*n* = 134)	Vegetated plots (*n* = 67)	All sub-quadrats (*n* = 2144)	Vegetated sub-quadrats (*n* = 1072)
Asteraceae							
***Achillea millefolium* L.**	25.78	0.33	78.75	21.6%	43.3%	7.9%	15.8%
***Anaphalis margaritacea* L.**	2.53	0.02	143.52	9.7%	19.4%	1.7%	3.4%
***Solidago sempervirens* L.**	34.18	0.32	108.16	14.2%	28.4%	3.5%	7.0%
***Symphyotrichum novi-belgii* L.**	2.06	0.02	115.84	5.2%	10.4%	1.7%	3.4%
Brassicaceae							
***Cakile edentula* (Bigelow) Hook.**	10.71	0.05	228.8	0.7%	1.5%	0.3%	0.7%
Caryophyllaceae							
***Honckenya peploides* L.**	1.12	0.01	91.64	11.9%	23.9%	2.9%	5.9%
***Moehringia lateriflora* (L.) Fenzl**	0.6	0.002*	1495	1.5%	3.0%	0.2%	0.5%
***Stellaria graminea* L.**	0.3	0.008*	187.5	1.5%	3.0%	0.3%	0.6%
Cupressaceae							
***Juniperus communis* var. *megistocarpa* Fern. & St. John**	0.06	0.005*	60	0.7%	1.5%	0.7%	1.5%
***Juniperus horizontalis* Moench**	0.03	0.002*	65	1.5%	3.0%	0.4%	0.7%
Empetraceae							
***Empetrum nigrum* L.**	0.04	0.002*	95	3.0%	6.0%	2.2%	4.5%
Ericaceae							
***Calluna vulgaris* (L.) Hull**	0.01	0.001*	50	0.7%	1.5%	0.3%	0.7%
***Vaccinium angustifolium* Ait.**	0.78	0.01	134.14	3.7%	7.5%	2.2%	4.4%
***Vaccinium macrocarpon* Ait.**	0.18	0.008*	112.5	1.5%	3.0%	0.2%	0.5%
Fabaceae							
***Lathyrus japonicus* var. *maritimus* (L.) Kartesz & Gandhi**	5.34	0.03	185.56	20.1%	40.3%	9.5%	18.9%
Iridaceae							
***Sisyrinchium angustifolium* P. Mill.**	NA	NA	NA	0.7%	1.5%	0.1%	0.3%
Juncaceae							
***Juncus arcticus* var. *balticus* (Willd.) Trautv.**	9.58	0.32	30.34	3.7%	7.5%	2.1%	4.2%
***Spergularia salina* J.& K. Presl**	0.12	0.005*	120	2.2%	4.5%	0.4%	0.8%
Liliaceae							
***Maianthemum stellatum* (L.) Link**	18.43	0.21	88.68	6.7%	13.4%	1.1%	2.1%
Myricaceae							
***Myrica pensylvanica* Mirbel**	4.49	0.05	88.66	6.0%	11.9%	4.1%	8.1%
Onagraceae							
***Oenothera parviflora* L.**	9.78	0.07	142.51	6.7%	13.4%	0.8%	1.7%
Plantaginaceae							
***Plantago lanceolata* L.**	6.18	0.04	148.61	1.5%	3.0%	0.0%	0.0%
Poaceae							
***Ammophila breviligulata* Fern.**	30.54	0.3	101.14	53.0%	106.0%	36.0%	72.0%
***Festuca rubra* L.**	0.57	0.01	52.59	15.7%	31.3%	8.3%	16.6%
***Poa* spp.**	1.03	0.02	60.95	11.2%	22.4%	6.9%	13.8%
***Spartina pectinata* Bosc ex Link**	73.06	0.76	96.31	0.7%	1.5%	0.0%	0.0%
Polygonaceae							
***Rumex acetosella* L.**	1.34	0.01	180.54	2.2%	4.5%	1.2%	2.4%
***Rumex crispus* L.**	46.21	0.28	164.92	0.7%	1.5%	0.0%	0.0%
Primulaceae							
***Trientalis borealis* Raf.**	1.05	0.005*	210	0.7%	1.5%	0.2%	0.4%
Ranunculaceae							
***Thalictrum pubescens* Pursh**	5.36	0.05	106.41	0.7%	1.5%	0.4%	0.8%
Rosaceae							
***Fragaria virginiana* Duchesne**	12.44	0.13	96.11	3.7%	7.5%	2.0%	3.9%
***Photinia floribunda* (Lindl.) Robertson & Phipps**	4.55	0.06	79.2	3.0%	6.0%	0.1%	0.3%
***Rosa virginiana* P. Mill.**	11.22	0.14	81.21	9.7%	19.4%	4.9%	9.9%
***Sibbaldiopsis tridentate* (Ait.) Rydb.**	2.96	0.04	82.33	1.5%	3.0%	1.1%	2.2%
Scrophulariaceae							
***Rhinanthus minor* L.**	0.87	0.01	145.67	2.2%	4.5%	0.2%	0.4%

*Samples with low weights

**All SLA values were calculated from unrounded values.

Table 3.2: Results of an indicator species analysis using three groups of sampling plots determined by hierarchical cluster analysis. The indicator values (*IV*) and *p* values are given for each significant indicator species. Perfect indicator species are in bold. No species were significant indicators of group 1. Relative abundance for a species in the group of which it is an indicator species, was calculated by average abundance of a given species in a group of plots divided by the average abundance of that species in all plots expressed as a percent.

	IV	***p* value**	**Group membership of indicator species**	**Relative abundance in group**
Achillea millefolium	68.9	0.002	2	69
Anaphalis margaritacea	52.3	0.001	3	90
Empetrum nigrum	**33.3**	**0.006**	**3**	**100**
Festuca rubra	88.2	0.001	3	88
Fragaria virginiana	**41.7**	**0.001**	**3**	**100**
Juncus arcticus* var. *balticus	**33.3**	**0.004**	**3**	**100**
Lathyrus japonicus var. *maritimus*	51.3	0.004	2	66
Myrica pensylvanica	57.6	0.001	3	99
Poa spp.	97.1	0.001	2	97
Rosa virginiana	47.9	0.004	3	72
Rumex acetosella	**25.0**	**0.025**	**3**	**100**
Symphyotrichum novi-belgii	**41.7**	**0.004**	**3**	**100**
Vaccinium angustifolium	**41.7**	**0.002**	**3**	**100**

Table 3.3: Correlation coefficients showing environmental variables with Axis 1 and Axis 2 of the NMDS ordination. Stronger correlations ($r > 0.25$) are shown in bold font.

Environmental variables	Axis 1	Axis 2	Group association
elevation	-0.18	0.08	2
meters from south shore	-0.06	**-0.26**	**1**
meters from north shore	**0.45**	0.16	**3**
presence of organic layer	0.18	**0.46**	**2**
evidence of grazing	0.22	**0.28**	**2,3**

Table 3.4: Correlation coefficients showing correlations of abundance-weighted plant traits with Axis 1 and Axis 2 of the NMDS ordination. Stronger correlations ($r \geq 0.5$) are in bold font.

Abundance weighted traits	Axis 1	Axis 2	Group association
Ramet type			
clumped ramet	-0.07	-0.45	1,3
spreading ramet	-0.17	0.34	1,2
dispersed ramet	0.41	0.40	3
Raunkiær plant life-form			
geophytes	-0.24	**0.57**	1,2
phanerophytes	0.41	0.40	3
chamaephytes	**0.77**	**-0.03**	**3**
hemicryptophytes	**-0.57**	**-0.45**	**1**
therophytes	0.05	-0.36	1,3
Specific leaf area values			
30 - 65	**0.50**	**0.13**	**3**
78 - 120	-0.21	-0.45	1
134 - 148	**0.61**	**-0.03**	**3**
164 - 228	-0.32	0.53	2
Plant heights			
short (2 – 11 cm)	**0.80**	**0.03**	**3**
medium (14 – 29 cm)	**0.58**	**0.34**	**3**
tall (35 – 124 cm)	**-0.76**	**-0.47**	**1**
Boolean traits			
perennial	-0.42	0.38	1,2
creeping or fibrous roots	-0.01	-0.48	1,3
waxy or succulent leaves	-0.22	0.35	1,2

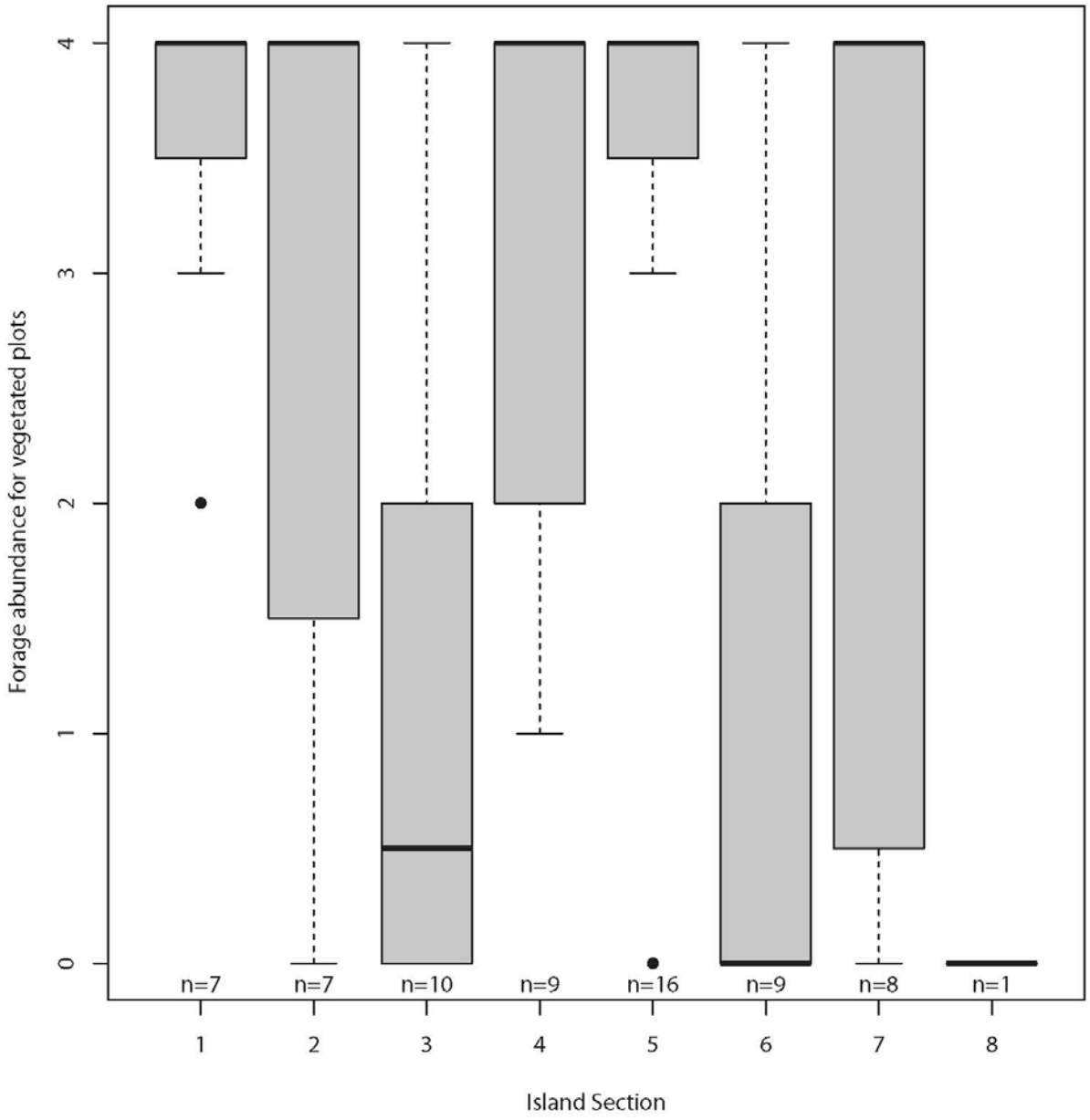

Figure 3.1: Distribution of vegetated plots (*n* = number of vegetated plots in each Island Section) across different categories of grazing evidence (0 = no evidence, 4 = abundant evidence) implying forage abundance for each of the 8 sections on the island. Although these sections are sequential, this data does not imply a longitudinal gradient. Boxes encompass the 25%–75% quartiles of the data, with the median indicated by the thick line through the center of each box. Whiskers extending from the box encompass the 95% quartiles, and extreme observations are shown as black filled circles.

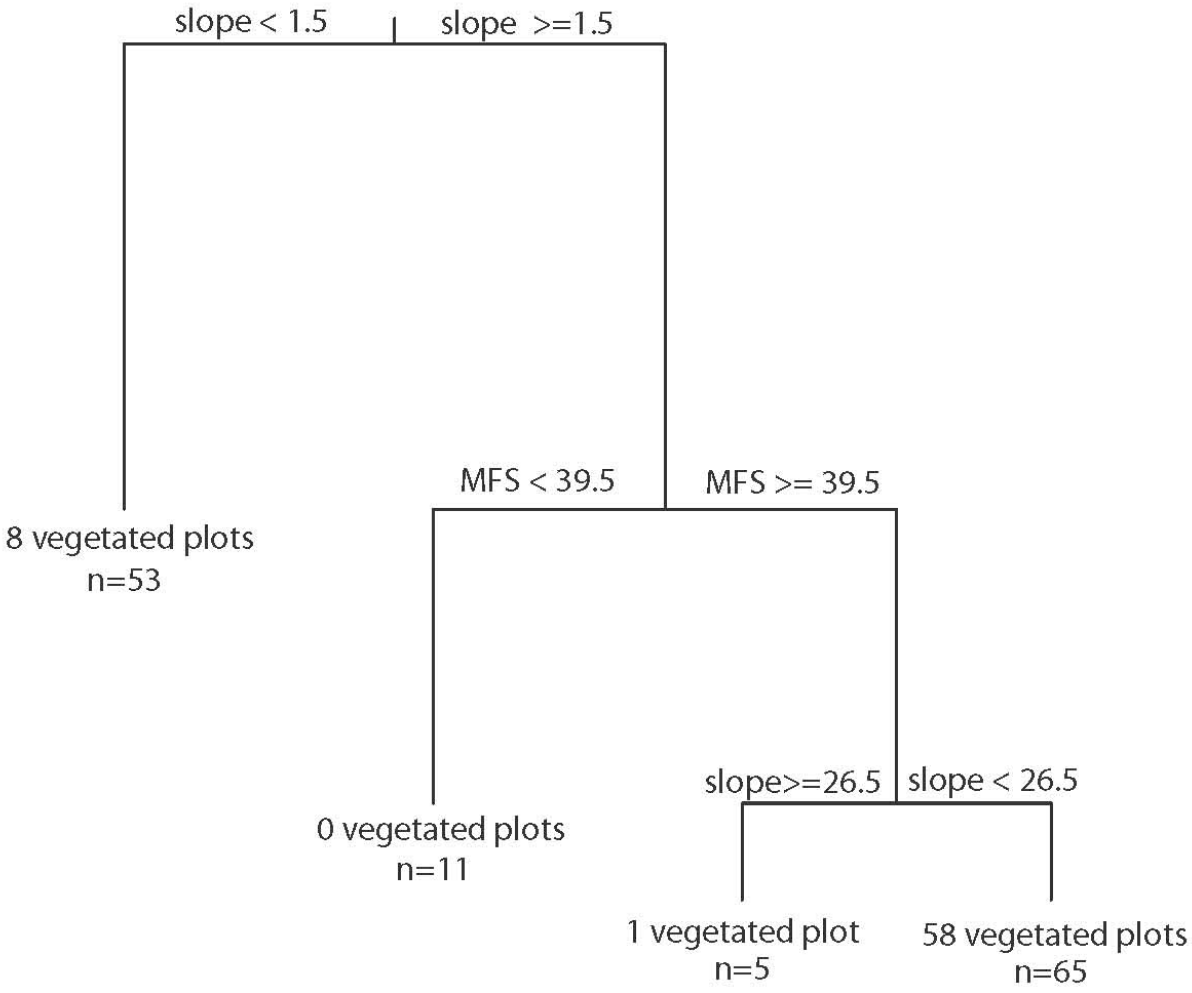

Figure 3.2: Results of a regression tree analysis assessing environmental factors that influence whether a plot is vegetated or not (*n* = 134). Environmental predictor importance is measured by relative distance from the stem terminus to the root node at the top of the tree. The environmental threshold determining each node split is written on each branching event (slope = slope in degrees, MFS = meter from nearest shore). The vegetated plots (*n*) are given at the base of each terminal node as well as the number of plots falling into that group. The error was 0.41 and the cross validation error for this analysis was 0.60 (see Figure 3.3).

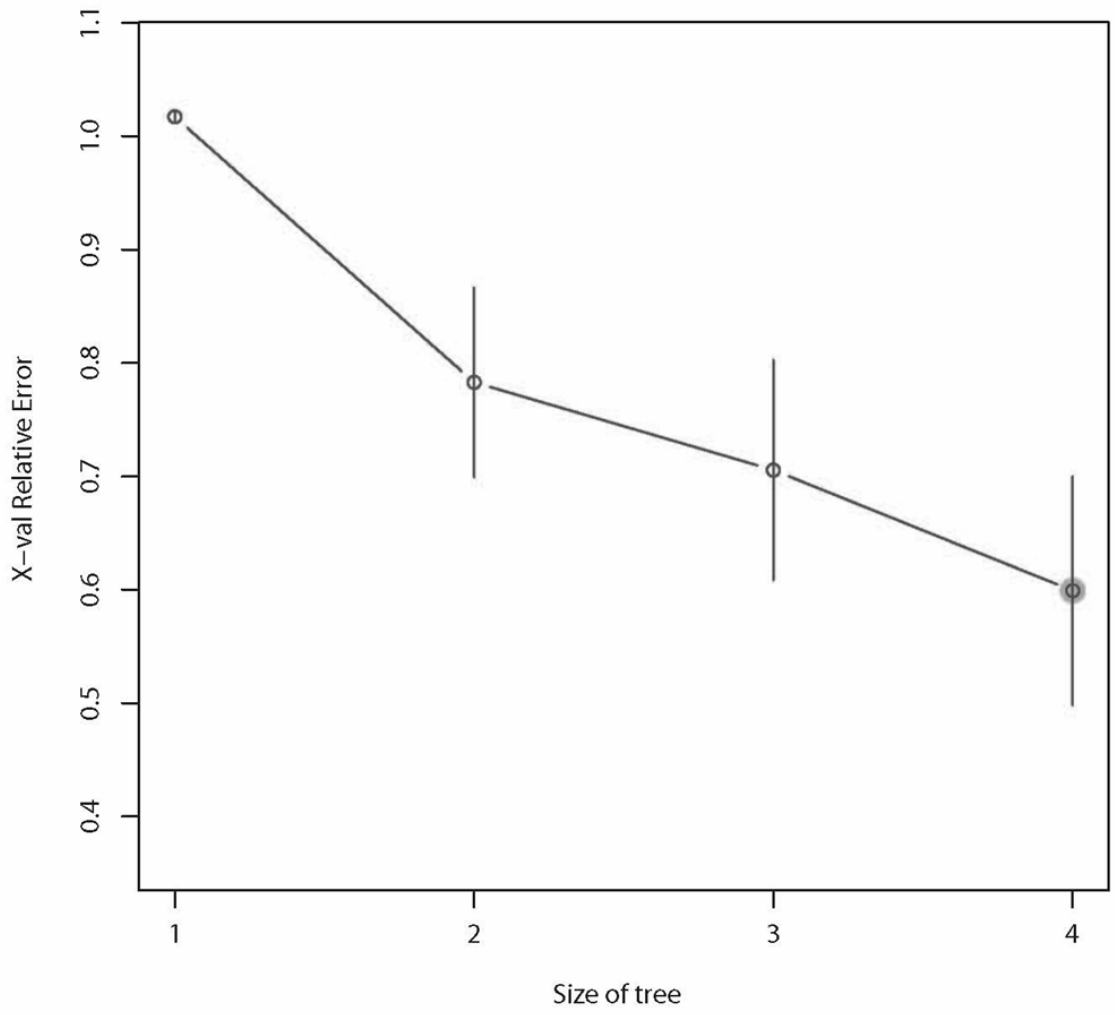

Figure 3.3: Cross validation results for the regression tree analysis assessing environmental factors influencing vegetation, to determine the optimal size of the tree. Error bars are estimated from random subsets of the samples. The grey solid point represents the number of terminal nodes with the lowest error.

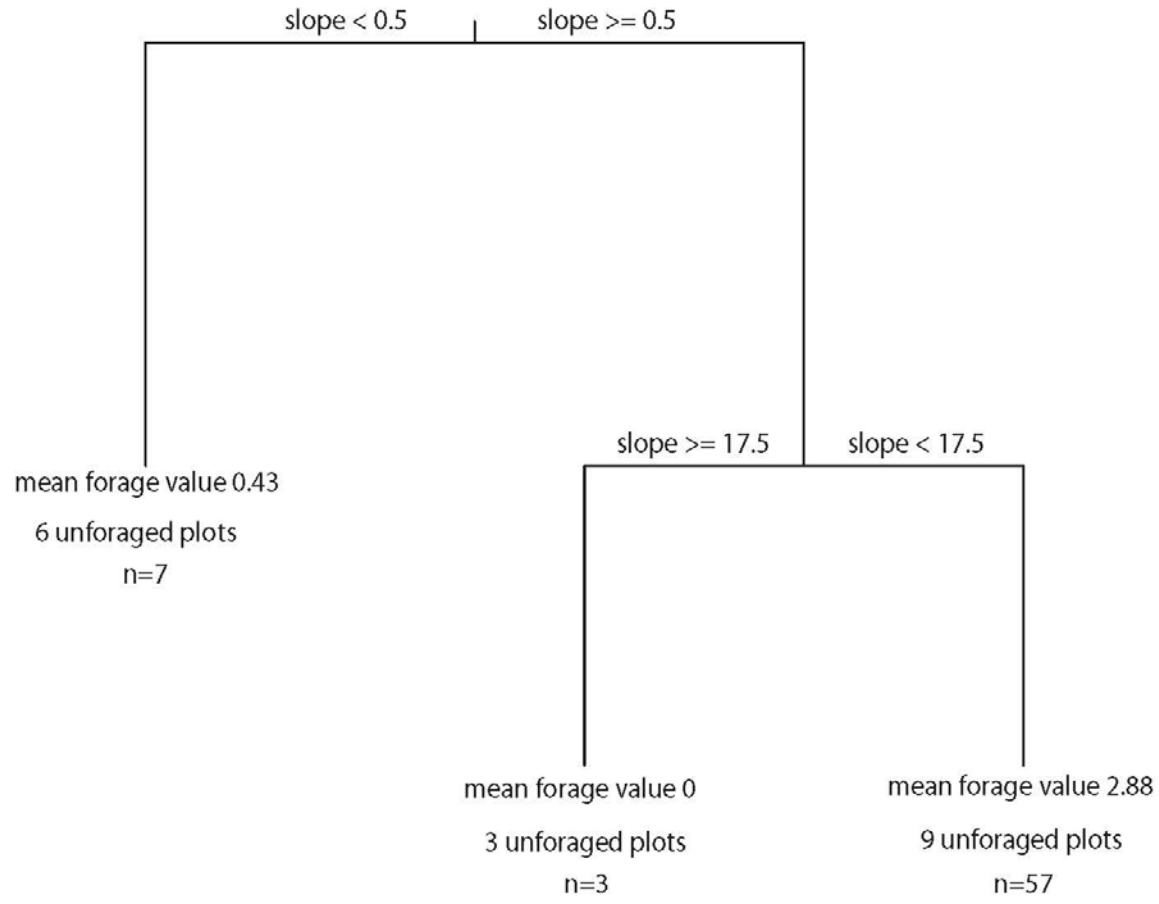

Figure 3.4: Results of a regression tree analysis assessing environmental factors that influence evidence of grazing (foraging) levels (n = 67). Environmental predictor importance is measured by relative distance from the terminus to the root node at the top of the tree. The environmental threshold determining each node split is written on each branching event (slope = slope in degrees). The mean value of grazing (forage) evidence levels (0 = no evidence, 4 = abundant evidence) for each group is given, along with number of grazed upon plots, and total group membership values at the base of each terminal node. The error was 0.71 (Figure 3.5) and the cross validation error for this analysis was 1.01.

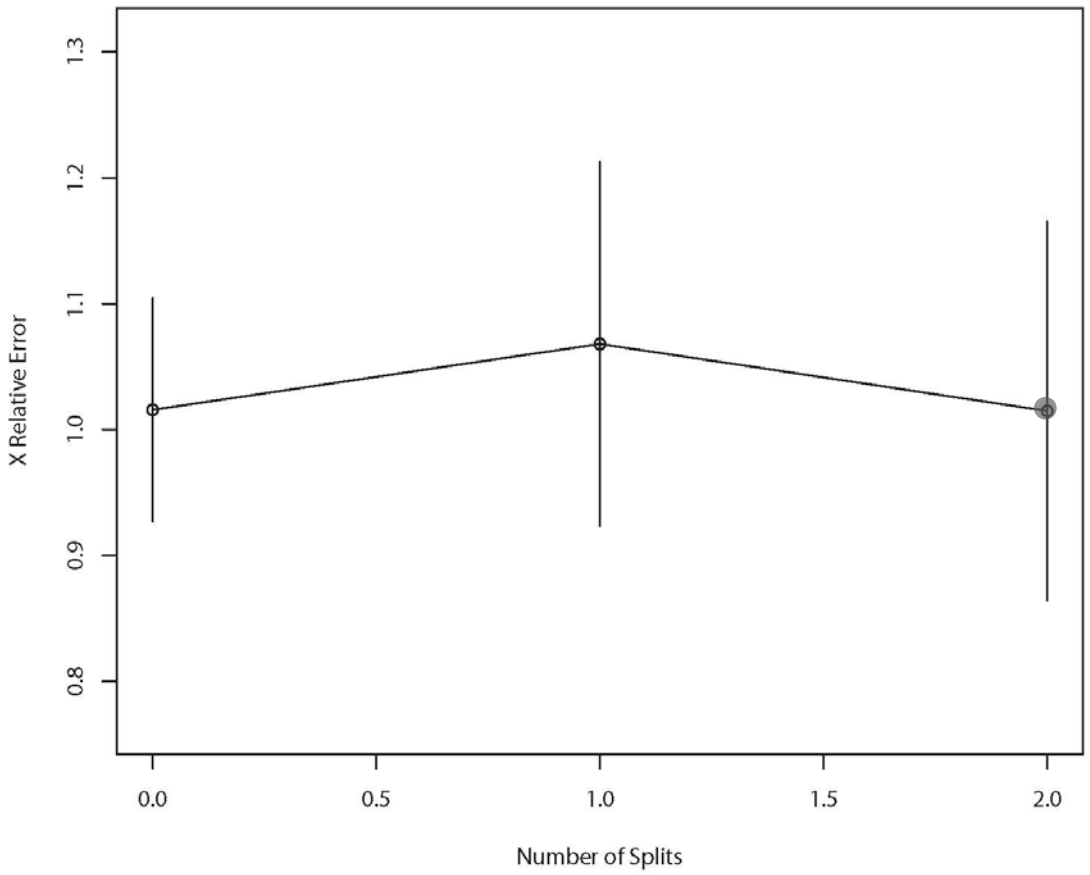

Figure 3.5: Cross validation results for the regression tree analysis assessing environmental factors influencing grazing pressure, to determine the optimal size of the tree. Error bars are estimated from random subsets of the samples. The grey solid point represents the number of terminal nodes with the lowest error.

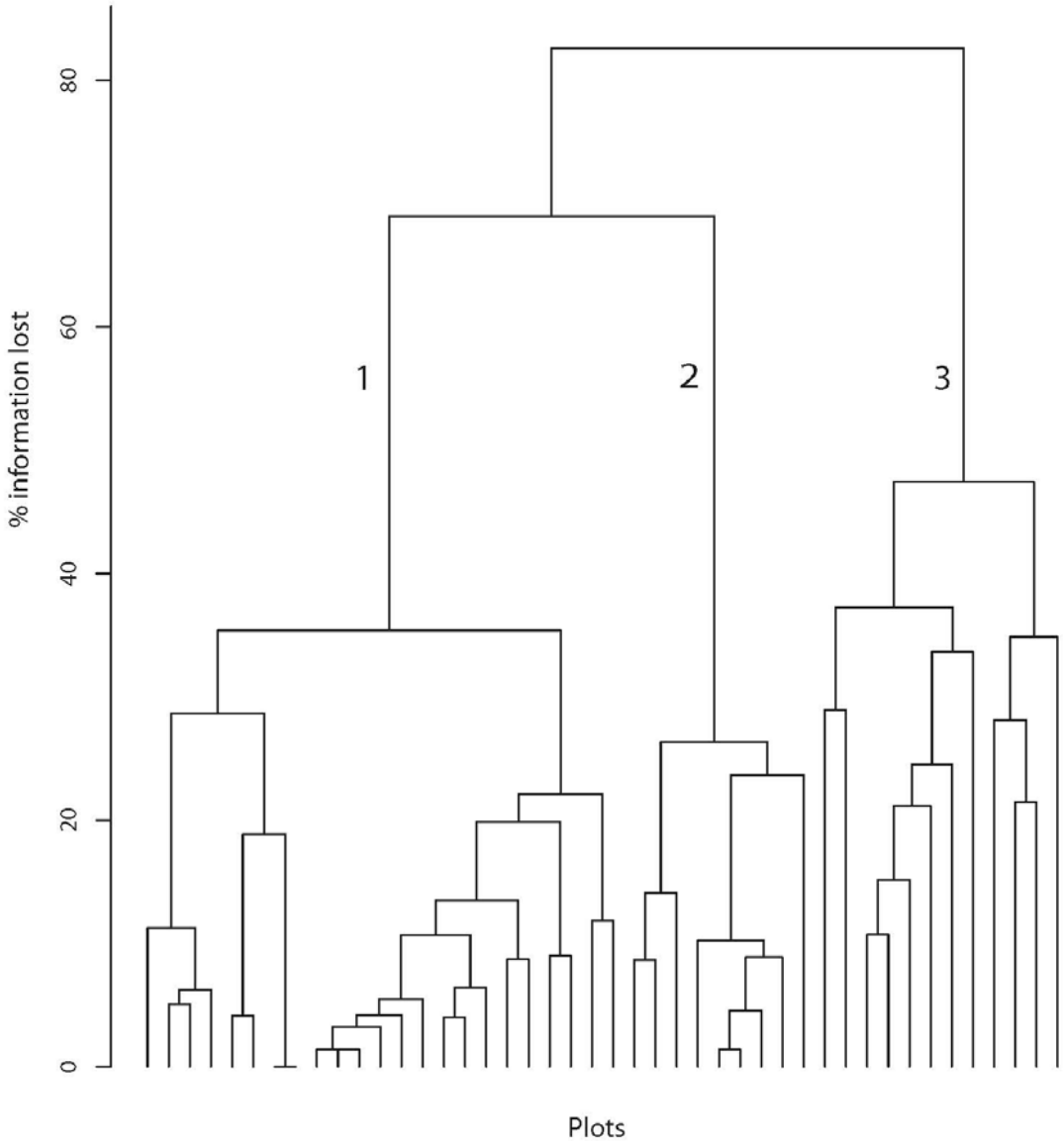

Figure 3.6: Hierarchical cluster analysis, using Ward's method, of plots based on vegetation composition (44 plots x 24 species). Each terminal branch represents one plot and the length of each line represents the distinctness of the merging event. The three main groups are labeled as 1, 2 and 3. Agglomerative coefficient = 0.866, chaining = 5.86%.

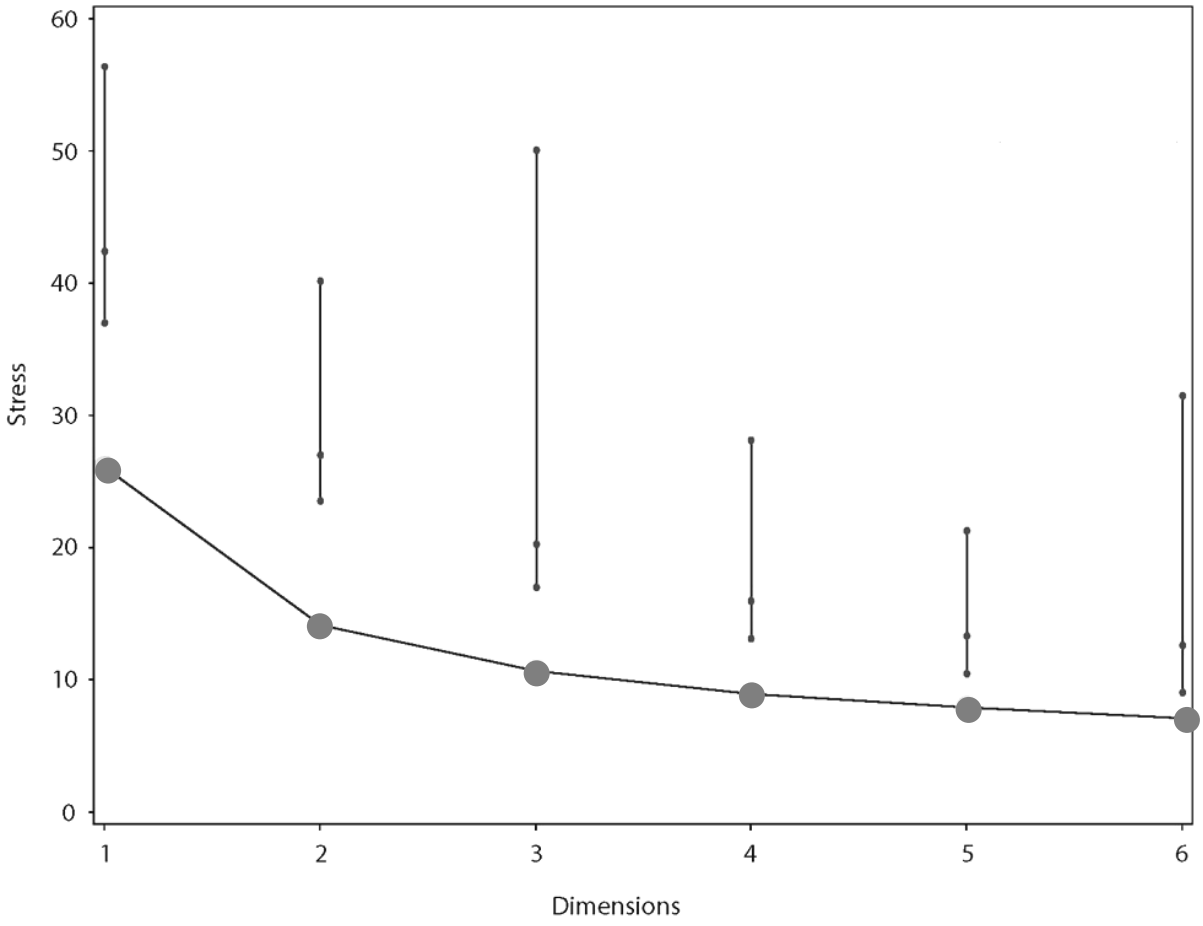

Figure 3.7: Scree plot for the NMDS ordination of sample plots showing changes in stress levels for solutions at different dimensions. Grey points represent real data. High, medium, and low small black points along a vertical lines represent the maximum, mean, and minimum stress for randomized data. The break in the slope of the stress line at 2 dimensions indicates the most succesful solution.

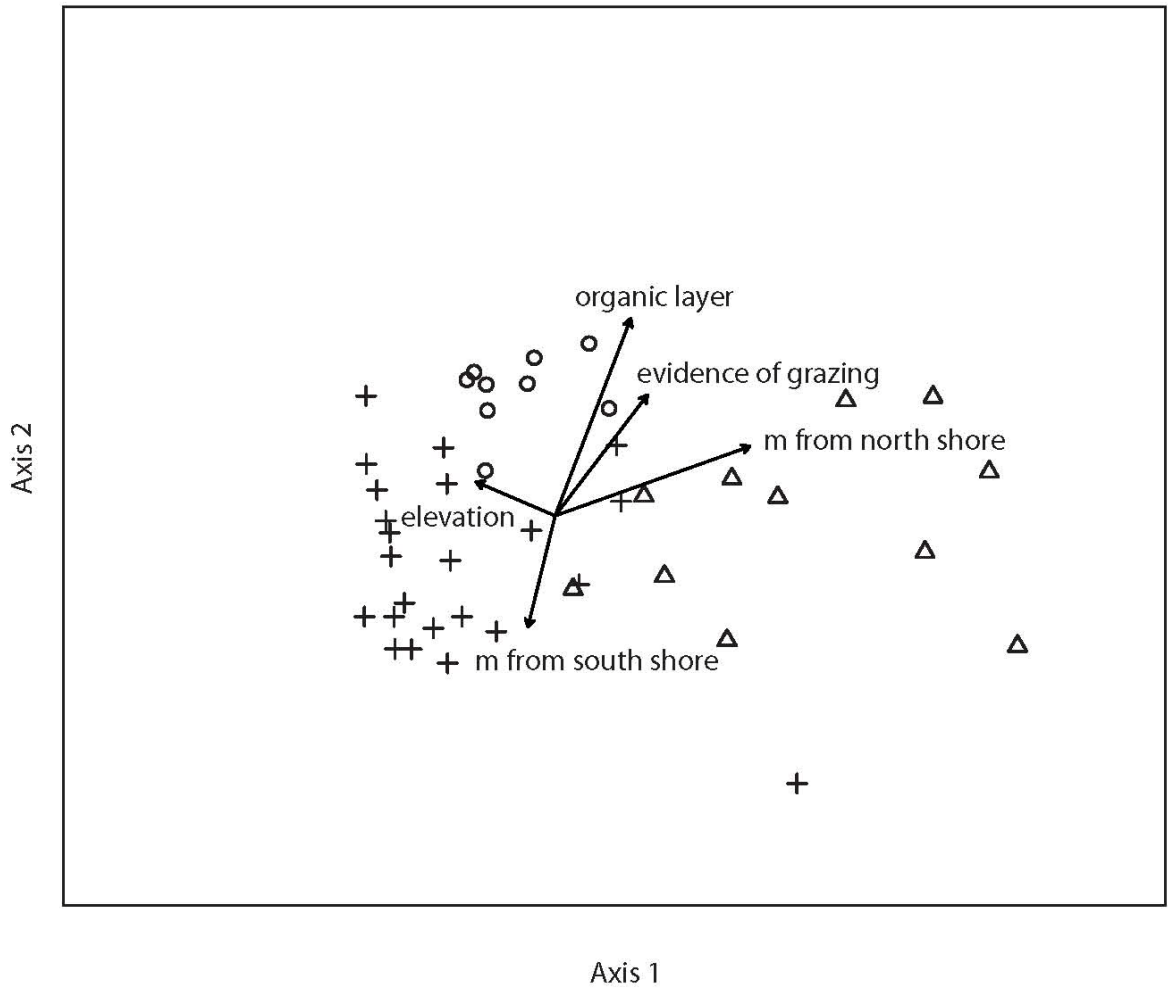

Figure 3.8: 2-dimensional ordination of plots in species-space (44 plots × 24 species). The ordination solution resulted in a maximum residual value of 0.00051, stress of 12.32, and non-linear goodness of fit of $r^2 = 0.985$. A post hoc test to determine the correlation coefficients between ordination and original distances in dissimilarity matrix revealed Axis 1 and 2 had r^2 values of 0.54 and 0.32, respectively. Each plot is represented in the graph by a symbol of a plus sign, circle, or triangle, which correspond to groups 1, 2, or 3 respectively of the cluster analysis. Distances between plots represent approximate differences in species composition between the plots. Environmental vector overlays are represented as black arrows where the angle represents the correlation with each axis and its length the strength of the correlations (see Table 3.3).

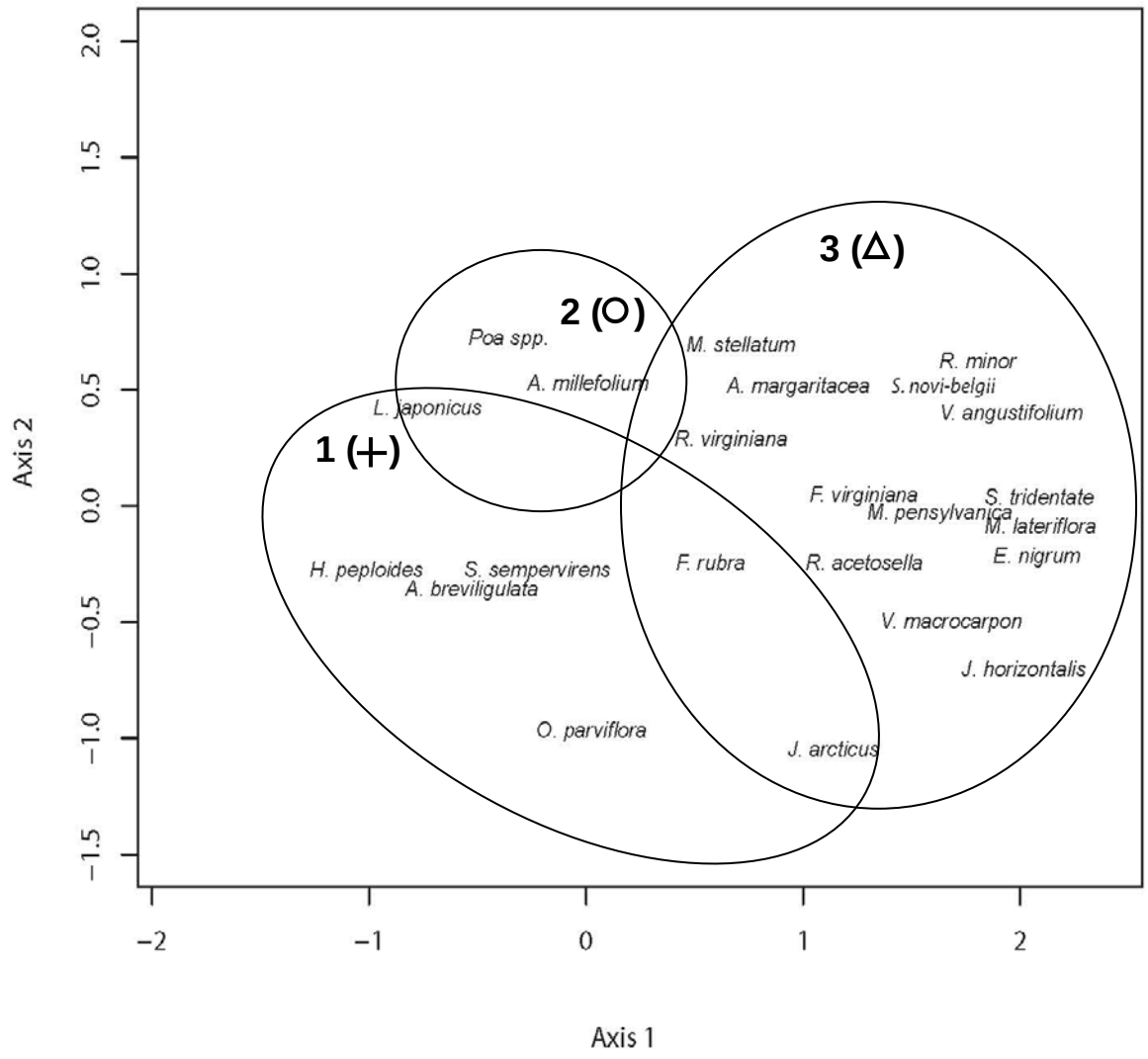

Figure 3.9: Ordination of species centroids along the axes of a 2-dimensional NMDS. Distances between species centroids represent approximate differences in abundance on the axes. Ellipses are drawn to represent approximate locations of the plot groups 1, 2, and 3 from the HCA analysis (Figure 3.6), or plus signs, circles and triangles, respectively in Figure 3.10.

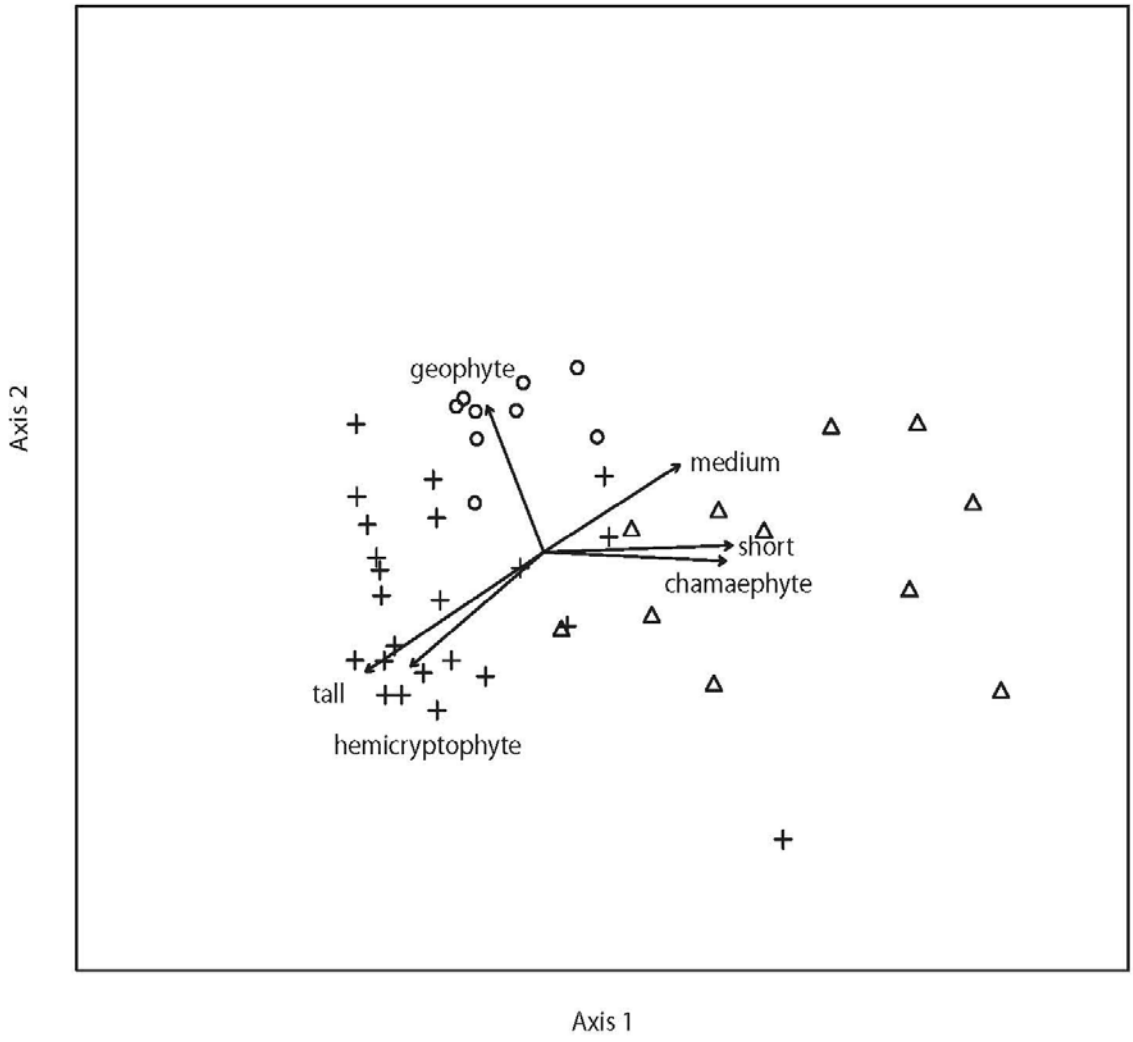

Figure 3.10: Plant height along with Raunkiaer's life-forms as plant trait vector overlays on a NMDS plot ordination of plots in species-space (44 plots × 24 species). Each plot is represented in the graph by either a plus sign, circle, or triangle, which correspond to groups 1, 2, or 3 respectively of the cluster analysis. Distances between plots represent approximate differences in species composition between the plots. Plant trait vector overlays are represented as black arrows where the angle represents the correlation with each axis and its length the strength of the correlations.

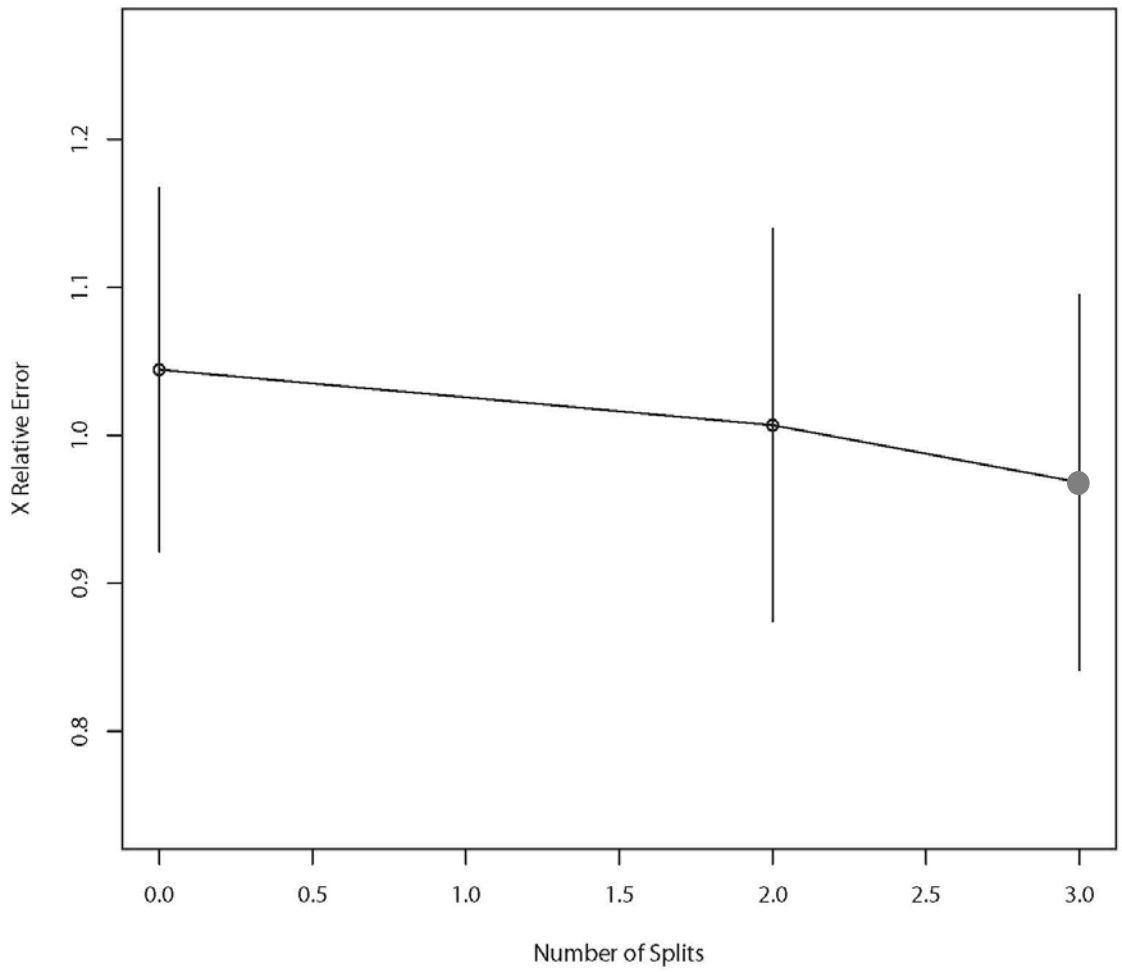

Figure 3.11: Cross validation results for multivariate regression tree of most common species distribution. Error bars are estimated from random subsets of the samples. The dark grey solid point represents the best number of nodes as it has the lowest cross validated relative error of 0.98.

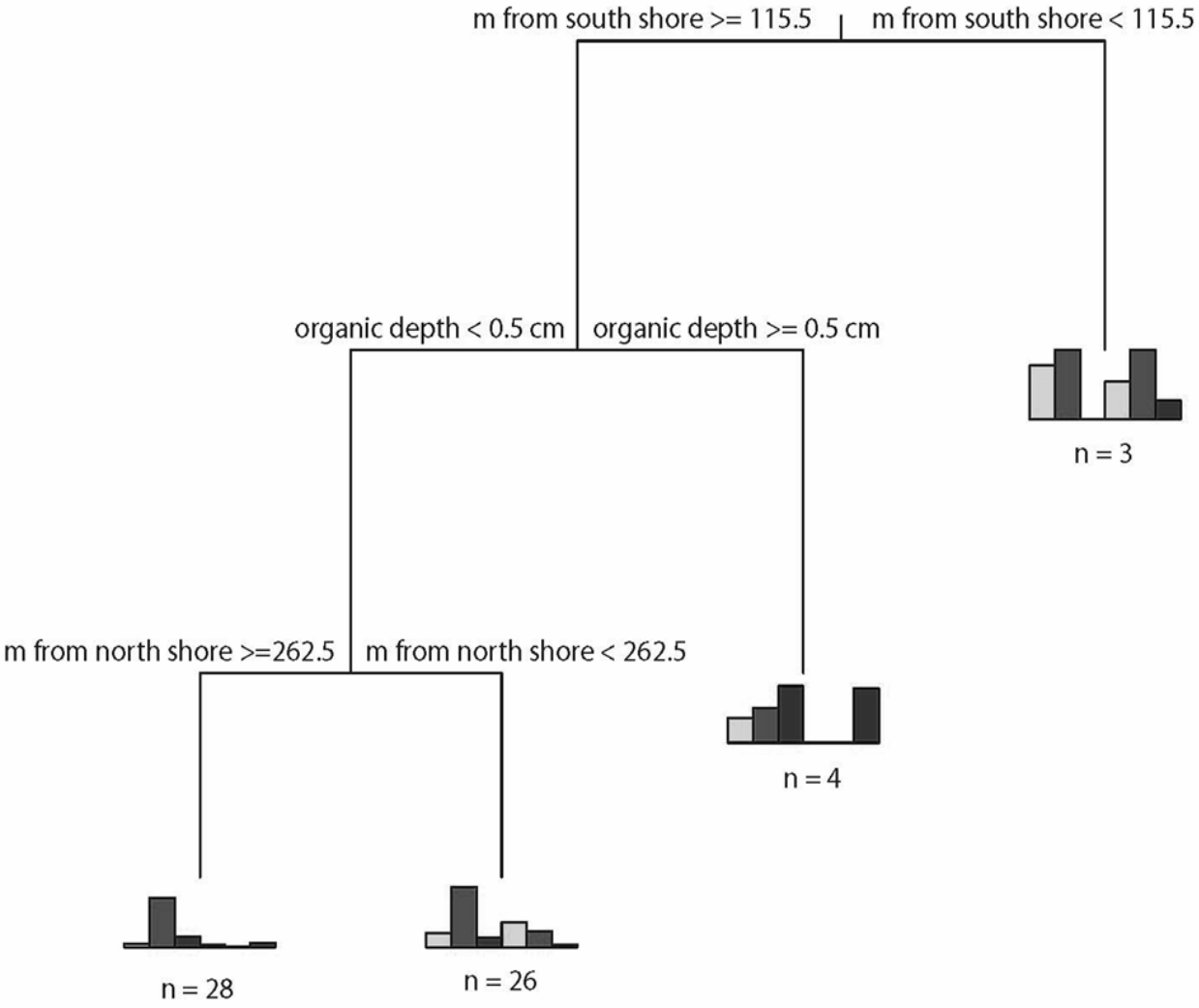

Figure 3.12: Multivariate regression tree relating patterns of abundance of the six most common species to measured environmental factors from 61 plots sampled on Sable Island. This tree identifies a single environmental variable as the indicator variable for each branching event terminating at a node that describes the vegetation composition it represents. Bar graphs located at terminal nodes show the average abundance of each species in that group of plots and the numbers under bar graphs represent the number of plots in the group (*n*). Each bar graph represents the following species, from left to right: *Achillea millefolium* var. *occidentalis*, *Ammophila breviligulata*, *Festuca rubra*, *Lathyrus japonicus* var. *maritimus*, *Poa*. spp and *Rosa virginiana*. Error for this tree is 0.69 and cross-validation error is 0.98.

4 DISCUSSION

Vegetation measurements obtained from 138 sample plots on Sable Island showed the presence of three general community types, plus unvegetated areas. The distribution of these vegetation associations were correlated with both measured environmental variables and plant traits. On Sable Island, plots found nearest the shoreline were unvegetated beaches where erosion, sand deposition, and tidal over-wash inhibit vegetation establishment and survival. As distance from shore increased, vegetation density increased where coastal stress was less severe. Slope greatly influenced vegetation establishment and further community development, and also affected forage evidence (grazing or browsing) levels.

4.1 VEGETATION GROUPS

Two methods of multivariate community analysis, each using different methods of comparison, revealed similar plot groupings which support the robustness of the three vegetation groups found. This number of groups are lower than past vegetation community investigations (Welsh 1975, Catling et al. 1984). Catling *et al.* (1984) named seven terrestrial communities and two aquatic communities: Sandwort, Marram-Forb, Marram, Marram-Fescue, Shrub heath, Cranberry heath, Pond edge Herbaceous, Brackish ponds, and Freshwater ponds. The seven terrestrial groups were subjectively distinguished based on dominant species or groups of dominant species (Catling et al. 1984).

An important difference between my research and previous vegetation studies on Sable Island was the use of stratified random sampling and subsequent objective analyses across different gradients, rather than subjectively identifying vegetation communities in the field. My study did not capture the full range of vegetation types documented by other research on the island (St. John 1921, Welsh 1975, Catling et al. 1984, Stalter and Lamont 2006). However, the results of the study have a strong empirical basis in representing the dominant vegetation cover of Sable Island because of the large number of randomly distributed plots that were sampled across the length and width of the island. For comparisons between studies, four of the seven community types defined by Catling *et al.* (1984) can be consolidated into one of the three groups defined in my analyses. My sampling scheme did not capture the remaining three of the vegetation groups identified by Catling *et al.*(1984) either because I specifically sampled only terrestrial vegetation (omitting Brackish and Freshwater Pond groups) or my sampling plots simply did not chance to fall in a certain vegetation type (Pond edge herbaceous) that was likely rare on the island. In addition, many of my plots represent communities that are compositionally intermediate between the distinct groups that Catling *et al.* (1984) identified.

Group 1 plots from my analysis occupied areas located along the east and west extremities of the island, as well as the south shore, where sand and salt stress were likely to be highest (Figure 4.1). Plants well suited to sand disturbance and salt exposures were most abundant in these plots. For example, *Ammophila breviligulata* growth is promoted by sand burial (Disraeli 1984). *Solidago sempervirens L.* is known to be very tolerant of salt spray (Cartica and Quinn 1980). These two species were commonly found in the vegetation communities represented by group 1 (Figure 3.11). Vegetation in this group was generally tall with high energy investment in stems and support structures. Group 1 had specific leaf area

(SLA) values between 78 and 120. These moderately high values of SLA are correlated with increased structural defenses (e.g. woodiness, thorns, or less digestible content,) against generalist herbivores (Kraft and Ackerly 2010). Group 1 was strongly correlated with the hemicryptophyte life form (Figure 3.12), which is a typical life form for plants in the first stages of vegetation succession (Trabaud 1987). Herbaceous hemicryptophytes have germination characteristics that are more adapted to colonization of open sites (Luna and Moreno 2009) such as coastal dune ecosystems. Sandwort and Marram groups from Catling *et al.* (Catling et al. 1984) could both be considered part of group 1.

Group 2 plots were located away from the eastern and western extremities of the island and dispersed throughout the center regions on more stable dune systems (Figures 3.10 and 4.1). Common species in these plots included *Lathyrus japonicus, Achillea millefolium,* and *Anaphalis margaritacea* which are all geophyte life forms. Geophytes are well suited to this intermediate stress location because their underground storage organs enable the plants to survive adverse conditions such as drought, cold temperatures, and heavy grazing (Noy-Meir and Sternberg 1999). Waxy leaves are another strategy that reduces water loss in harsh conditions. Both *Lathyrus japonicus* and *Maianthemum stellatum* have waxy leaves and are common on Sable Island. Marram-Forb and Marram-Fescue (Catling et al. 1984) communities fit into group 2.

Group 3 communities were the least tolerant of sand and salt disturbances, and were located away from the east and west extremities of Sable Island similar to group 2. This group was correlated with distance from the north shore which is a more sheltered environment. Group 3 contained heath species such as *Empetrum nigrum, Myrica pensylvanica,* and *Vaccinium angustifolium.* Shrub heath and Cranberry heath (Catling et al. 1984) community types fall under group 3. These vegetation communities had more woody species than the previous two groups

and showed signs of past (winter) browsing activity in the form of clipped woody stems, rather than fresh browsing evidence. These woody species typically grew quite low to the ground either because of browse effects, as evident in *Myrica pensylvanica* and *Vaccinium angustifolium,* or because their decumbent growth structure limited vertical growth, as with *Juniperus horizontalis* and *Juniperus communis.* Group 3 communities were most strongly correlated with the chamaephyte life form, whose germination is associated with closed-canopy vegetation (Luna and Moreno 2009) and are more typically found later in succession (Kazanis and Arianoutsou 1996). Plants in this group spanned the short and medium height ranges, minimizing the energy costs associated with taller biomass. Plants in this group also had moderately high (*Vaccinium angustifolium)* and the lowest (*Juniperus horizontalis)* SLA values. SLA values that are low indicate plants that conserve nutrients by not investing as much energy in fast biomass production (short plants or plants with evergreen or small leaves), whereas higher SLA indicates plants whose strategy is rapid biomass production (tall, leaf, and deciduous plants). It seems both strategies are beneficial in group 3 where very high SLA strategies are not necessary because these plants occur in areas of lower stress.

4.2 DUNE SUCCESSION ON SABLE ISLAND

To study succession (long-term ecological change), without using a chronosequence approach, an area must be monitored over a longer period of time than my project could capture. This project may provide baseline data for future investigations. Results from my vegetation description along disturbance gradients can, along with personal observations, suggest plausible

hypothesis of dune succession that could be tested with further research. It is my view that dune succession on Sable Island is not linear as Cowles (1899) suggested along Lake Michigan's sand dunes. While there were correlations between each vegetation group and certain environmental variables, all three groups of communities were represented throughout the center region of the island (Figure 4.1). This implies that all stages of succession may occur throughout the majority of Sable Island due to various disturbance types (e.g. sand erosion and accretion, slope, grazing, wind, salt spray, etc.) and disturbance severity (Miyanishi and A. Johnson 2007).

As Catling *et al.* (1984) predicted, many successional trajectories are possible depending on the disturbances and environmental conditions each community is subjected to (Figure 4.2). The most important environmental gradients influencing vegetation community composition found in my analysis (slope and distance from shore) are associated with sand movement (i.e. accumulation or erosion) which Catling *et al.* (1984) also recognized as important drivers for succession on Sable Island.

Vegetation is sorted along these gradients. Greater numbers of sand-sensitive species occur where there is less sand input. Therefore, group 3 may be deemed "mature" because an area containing this community type experiences the least environmental stress allowing a longer time period for the community to develop. Group 1 consisting of mostly pioneer species, was the only community observed along the shores and narrow sand spits of the east and west extremities (Figure 4.1). These areas experience the greatest disturbances as there is little protection from wind and waves. Almost continuous environmental stress does not allow less tolerant species to establish on these sand spits. With constant sand and salt input to the system, *Ammophila breviligulata* and *Honckenya peploides* dominated communities (group 1) should maintain their successional stage (Figure 4.2) and could be considered a stable community under those

environmental conditions. Group 2 might be considered a transitional community type, through which a community could pass before becoming group 3 if stress continues to decrease, as these plants are moderately tolerant of sand and salt stress. A simplified successional schematic using only the three groups of this study (Figure 4.3) and overall stress input to an ecosystem represents the successional trajectory I understand to exist on the dunes of Sable Island.

4.3 TRENDS IN EVIDENCE OF GRAZING

Evidence of grazing varied across island sections which may be explained by various abiotic factors as well as horse population densities. It is possible that trends for specific plant species may be observed when confounding variables, such as horse density, are considered (e.g., in response to density-dependent habitat selection (Rosenzweig 1981, 1991); however, this was beyond the scope of my study. Island sections three and six, with lower grazing-evidence levels than other sections, had steep slopes and great variation in topography which may make travel and gaining access to high vegetated areas difficult for horses. Section eight was a long and narrow sand spit that provided little shelter from the wind and ocean. This section frequently received over-washed from waves and was isolated from the main part of the island. Although horses occasionally visited section eight, few were observed in 2010 - 2011 (E. Tissier and A. Contasti personal observations). All three sections with low grazing pressure had limited water resources where the horses must dig a water hole down to the water table to drink (E. Tissier and A. Contasti personal observation). These results are also likely to reflect spatial heterogeneity in

densities of horses across the island, which will be examined in future studies within the McLoughlin lab at the University of Saskatchewan, as my foraging data is preliminary.

One study has shown overgrazing and dune erosion as problems due to a horse population on Assateague Island, off the eastern coast of Maryland and Virginia, USA (Seliskar 2003). However, no vegetation community was observed to be grazed beyond potential recovery on Sable Island during the peak growing season (personal observation). Assateague Island is not comparable to Sable Island because it is a barrier island and has high human presence. Sable Island is located far from any mainland increasing the fetch (distance over which wind can act on water—increasing fetch yields increasing wind speed and wave energy) for all Sable Island's coastlines. Relationships found between vegetation and horses on Assateague may not be applicable to those on Sable Island.

Ammophila breviligulata on Sable Island is stimulated by both grazing and sand accumulation (Welsh 1975). However, this species declines in vigor and often remains vegetative on stabilized sand dunes where sand deposition is less (Marshall 1965) rendering this species particularly well suited to the similar biological stresses of both sand accumulation and foraging. Mowing and grazing are traditional management techniques for coastal dunes in The Netherlands (Grootjans et al. 2002) whose dune vegetation is similarly stimulated by disturbances. This method is most efficient in sustaining pioneer stages, which best retain sand and stabilizes dunes, especially in areas where nutrient cycling is still low such as in dune soils (Grootjans et al. 2002). Across the eight island sections, evidence of grazing was lowest in sections with the most elevation variation (sections three and six), as well as in section eight which is very narrow and frequently over-washed by waves. Slope and distance to shore were the

two most important variables restricting plant establishment, therefore it would make sense that with a decrease in vegetation, and increase coastal stress, grazing pressure would also be lower.

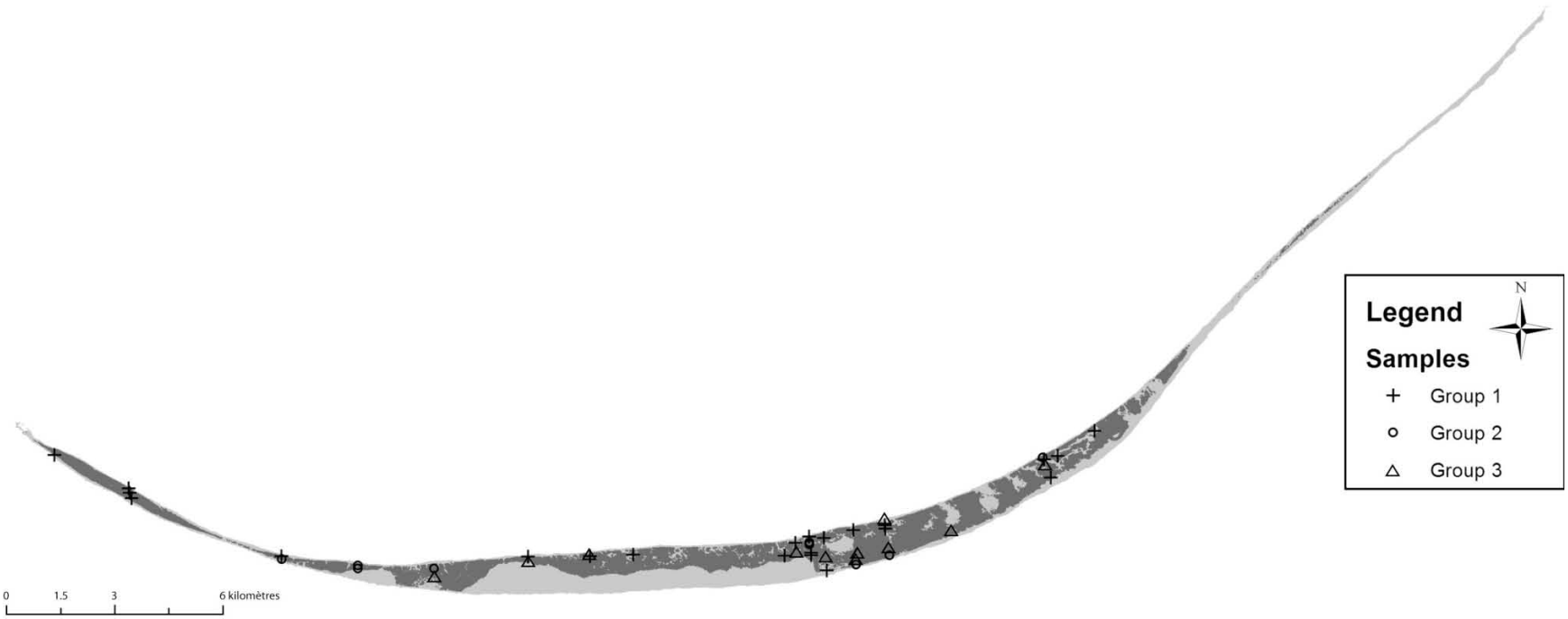

Figure 4.1: Plot locations of the three different vegetation communities on Sable Island. Dark grey areas are vegetated and light grey areas are unvegetated.

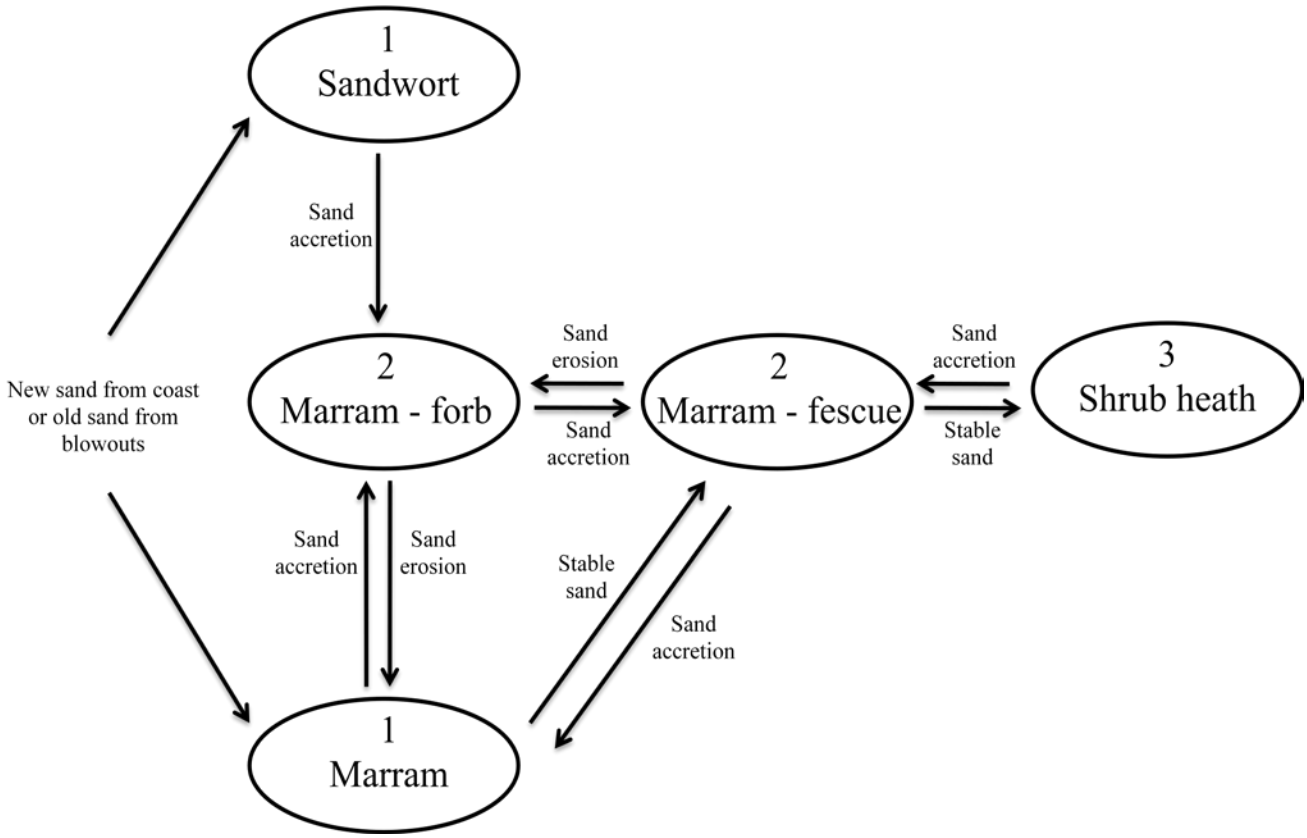

Figure 4.2: Successional possibilities of Sable Island dune systems modified from Catling *et al.* (1984). Arrows represent successional trajectories from one community type to another. The numbers represent the three community types found in this study and Catling's groups are written in the circles as well. This scheme represents terrestrial succession and does not include ponds or pond edges.

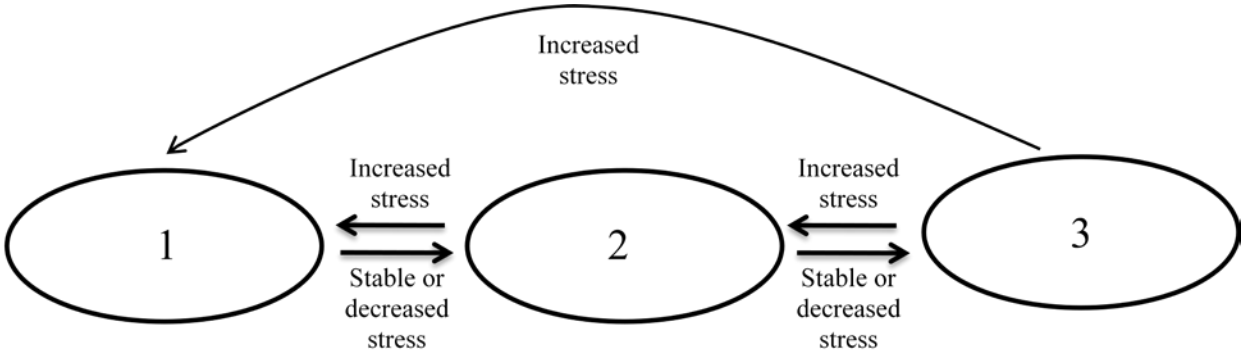

Figure 4.3: Successional possibilities using the three community types from this study (Represented as 1, 2, or 3). Succession is hypothesized to follow the arrows, given the condition associated with the arrow.

5 CONCLUSION

Plants occupying coastal dunes are affected by a number of factors such as wave over-wash, sand supply, wind and wave fetch, salt, and biogeographic factors like latitude. This applies to mainland coasts as well as islands. Barrier islands that are close to shore have been studied in many latitudes (Grootjans et al. 2002, Silva et al. 2008). Stress exposure on these islands is primarily from the ocean direction as opposed to the mainland direction, causing landward dunes to contain more mature and rich plant communities (Roman and Nordstrom 1988). Sable Island differs from barrier islands because it is a sand island located far from mainland and therefore experiences most disturbance stressors from many directions. Evidence from this study that both distances from north and south shores are important to vegetation composition seems to be a strong indication that conditions are different on Sable than mainland coasts. This multi-directional stress affects the distribution of the most mature communities (group 3) on Sable because there is no predictable landward dune to serve as prime habitat. Rather, the most mature communities are generally distributed further away from the greatest sand and salt disturbances and dispersed in various sheltered locations towards center portions of the island.

Strong disturbance forces acting from multiple directions cause vegetation succession to be less linear on Sable than on mainland or barrier island coasts. This is important for managers to recognize because mainland or barrier management techniques might not be successful for Sable Island's unique situation. For example, greater protection should be given to inland areas of Sable Island such as steep slopes and blowouts, as these have the potential to disperse sand onto less tolerant mature communities.

The effects of global warming will alter ocean and coastal environments, which will likely alter the abiotic stress to vegetated communities on Sable Island. Although estimates vary, global sea level rise is expected to rise 0.5 meters by 2100, and the frequency and strength of severe storms in the North Atlantic is increasing (IPCC 2007). Sea-level rise is a dominant force driving widespread coastal erosion (Leatherman et al. 2000) and because the greatest disturbance to Sable Island occurs during strong storms, the increase of these occurrences might serve to further filter the vegetation communities by selectively eliminating species less tolerant of sand and salt disturbances, reducing the relative abundance of these less tolerant species (group 3), and increasing the abundance of tolerant and sand-dependent species (group 1). Erosion reduces the area available for plant and animal communities (Feagin et al. 2005) and restricts the plant community's habitat to a narrow zone. Because it is not well understood what the ecological ramifications of this type of erosion to plant communities may be in terms of successional dynamics among species and functional groups, this study provides important preliminary data to understand the impacts of different gradients on island coastal dune communities.

Group 3 shrub heath communities are used by the horse population as well as rare birds, such as Roseate Terns and the Ipswich Sparrow (Ross 1980, Gochfeld 1983), which nests exclusively on Sable. Ipswich Sparrow and Roseate Tern are classified as Special Concern and Endangered, respectively, under the Species at Risk Act. This community type provides likely winter forage and protection for the horses (Welsh 1975), and in the summer months sparrows and Common Arctic terns also nest in group 3 areas. Shrub heath vegetation communities contained the most successful colonies because heath communities offered firm substrate against storm wash-outs and high vegetation for hiding from predators (Horn and Shepherd 1999). Thus, decreases in this vegetation type could negatively impact Sable Island’s terrestrial animals. Sea

level rise will also likely decrease the surface area of the island and increase stress further inland. Pioneer species represented in group 1 might shift to occupy more areas further inland that are presently group 2 and 3 communities.

The information I collected and synthesized during my study (2009–2011) will contribute to predicting of how Sable Island ecosystems may be altered with changes in future disturbance, including an increase in storm activity or change in sea level, both of which are predicted with climate change (Michener 1997, McInnes 2003). Knowing the different trajectories of dune succession and using approaches that allow my results to be compared with other studies will meet several important conservation strategies stated in Environment Canada's Conservation Strategy for Sable Island (Beson 1998) that have not yet been addressed by the scientific community. Grazing levels for key species reveals potential forage preferences from the horses on Sable, and can help future researchers understand what could influence habitat selection by the wild horse population. Linking vegetation patterns to succession allow for predictions of how forage quality and habitat use may change with future disturbance on the island. This is of particular importance presently as Sable Island management policies may be re-evaluated upon converting its statute from a Wildlife Sanctuary to a National Park.

6 LITERATURE CITED

Baas, A. C. W. 2007. Complex systems in aeolian geomorphology. Geomorphology **91**:311-331.

Bagnold, R. 1941. The Physics of Blown Sand and Desert Dunes. Methuen, London.

Bertness, M. 1999. The Ecology of Atlantic Shorelines. Sinauer Associates, Inc., Sunderland, MA, USA.

Beson, K. 1998. Towards a Conservation Strategy for Sable Island. Canadian Wildlife Service.

Brown, J. F. 1997. Effects of Experimental Burial on Survival, Growth, and Resource Allocation of Three Species of Dune Plants. Journal of Ecology **85**:151-158.

Byrne, M. L. and S. B. McCann. 1993. The internal structure of vegetated coastal sand dunes, Sable Island, Nova Scotia. Sedimentary Geology **84**:199-218.

Cameron, H. L. 1965. The Shifting Sands of Sable Island. Geographical Review **55**:463-476.

Campbell, L. 1994. Sable Island Shipwrecks, Disaster and Survival at the North Atlantic Graveyard. Nimbus Publishing Limited, Halifax, Nova Scotia.

Cartica, R. J. and J. A. Quinn. 1980. Responses of Populations of Solidago sempervirens (Compositae) to Salt Spray Across a Barrier Beach. American Journal of Botany **67**:1236-1242.

Catling, P. M., B. Freedman, and Z. Lucas. 1984. The vegetation and phytogeography of Sable Island, Nova Scotia. Proc. Nova Scotia Inst. Sci **34**.

Christie, B. J. 1995. The Horses of Sable Island. Pottersfield Press, Lawrencetown Beach, Nova Scotia.

Clarke, K. R., P. J. Somerfield, and M. G. Chapman. 2006. On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray–Curtis coefficient for denuded assemblages. Journal of Experimental Marine Biology and Ecology:55–80.

Collins, S. L. and D. E. Adams. 1983. Succession in grasslands: Thirty-two years of change in a central Oklahoma tallgrass prairie. Plant Ecology **51**:181-190.

Connell, J. H. 1978. Diversity in Tropical Rain Forests and Coral Reefs. Science **199**:1302-1310.

Cooper, W. S. 1967. Coastal dunes of California. Pages 119-124. Geological Society of America.

Cornelissen, J. H. C., S. Lavorel, E. Garnier , S. Diaz, N. Buchmann, D. E. Gurvich, P. B. Reich, H. t. Steege, H. D. Morgan, M. G. A. v. d. Heijden, J. G. Pausas, and H. Poorter. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian Journal of Botany **51**:335-380.

Cowles, H. C. 1899. The Ecological Relations of the Vegetation on the Sand Dunes of Lake Michigan. Part I-Geographical Relations of the Dune Floras. Botanical Gazette **27**:95-117.

Critchley, C. N. R. and S. M. C. Poulton. 1998. A method to optimize precision and scale in grassland monitoring. Journal of Vegetation Science **9**:837-846.

Daubenmire, R. F. 1974. Plants and environment. John Wiley and Sons, New York.

De'ath, G. 2002. Multivariate Regression Trees : A New Technique for Modeling Species-Environment Relationships. Ecology **83**:1105-1117.

De'ath, G. 2007. Boosted Trees for Ecological Modeling and Prediction. Ecology **88**:243-251.

De'ath, G. and K. E. Fabricius. 2000. Classification and regression trees: A powerful yet simple technique for ecological data analysis. Ecology **81**:3178-3192.

de Bonte, A. J., A. Boosten, H. G. J. M. van der Hagen, and K. V. Sýkora. 1999. Vegetation development influenced by grazing in the coastal dunes near The Hague, The Netherlands. Journal of Coastal Conservation **5**.

Disraeli, D. J. 1984. The Effect of Sand Deposits on the Growth and Morphology of Ammophila Breviligulata. Journal of Ecology **72**:145-154.

Dufrêne, M. and P. Legendre. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecological Monographs **67**:345-366.

Ehrenfeld, J. G. 1990. Dynamics and processes of barrier island vegetation. Reviews in Aquatic Sciences **2**.

Elstracke, R., editor. 1625. Hakjulutus posthumus or Purchas his pilgrimes: contayning a history of the world in sea voyages and lande travells by Englishmen and others. James MacLehose and Sons, Glasgow, UK.

Environment Canada. 2010. Canadian Climate Normals 1971-2000. Environment Canada.

Erskine, J. S. 1953. The ecology of Sable Island,1952. Proceedings of the Nova Scotia Institute of Science **23**.

Feagin, R. A., D. J. Sherman, and W. E. Grant. 2005. Coastal erosion, global sea-level rise, and the loss of sand dune plant habitats. Frontiers in Ecology and the Environment **3**:359-364.

Gagné, J.-M. and G. Houle. 2002. Factors responsible for Honckenya peploides (Caryophyllaceae) and Leymus mollis (Poaceae) spatial segregation on subarctic coastal dunes. American Journal of Botany **89**:479-485.

Gedge, K. E. and M. A. Maun. 1994. Compensatory Response of Two Dune Annuals to Simulated Browsing and Fruit Predation. Journal of Vegetation Science **5**:99-108.

Gilpin, J. B. 1858. Sable Island: its past history, present appearance, natural history. Wesleyan Conference Steam Press, Halifax, Nova Scotia.

Gleason, H. A. and A. Cronquist. 1991. Manual of the Vascular Plants of Northeastern United States and Adjacent Canada. Second Edition edition. New York Botinacal Garden, Bronx.

Gochfeld, M. 1983. The roseate tern: World distribution and status of a threatened species. Biological Conservation **25**:103-125.

Grootjans, A. P., H. W. T. Geelen, A. J. M. Jansen, and E. J. Lammerts. 2002. Restoration of coastal dune slacks in the Netherlands. Hydrobiologia **478**:181-203.

Harris, D. and A. J. Davy. 1986. Strandline Colonization by Elymus Farctus in Relation to Sand Mobility and Rabbit Grazing. Journal of Ecology **74**:1045-1056.

Horn, A. G. and P. Shepherd. 1999. Sable Island tern project 1998 final report. Unpublished report prepared for Sable Offshore Energy, Inc.

IPCC. 2007. Intergovernmental Panel on Climate Change Fourth Assessment Report: Climate Change

Irwin, E. H. R. 2003. Lighthouses and Lights of Nova Scotia. Nimbus Publishing, Halifax.

James, N. D. and D. J. Stanley. 1967. Sediment transport on Sable Island, Nova Scotia. Smithsonian Misc. Collections **152**.

James, N. D. and D. J. Stanley. 1968. Sable Island Bank Off Nova Scotia: Sediment Dispersal and Recent History. American Association of Petroleum Geologists Bulletin **52**:2208-2230.

Johnson, E. A. and K. Miyanishi. 2008. Testing the assumptions of chronosequences in succession. Ecology Letters **11**:419-431.

Kazanis, D. and M. Arianoutsou. 1996. Vegetation Composition in a Post-Fire Successional Gradient of *Pinus Halepensis* Forests in Attica, Greece. International Journal of Wildland Fire **6**:83-91.

Keddy, P. 1975. Botanical studies on Sable Island. Halifax, N.S.

Kraft, N. J. B. and D. D. Ackerly. 2010. Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. Ecological Monographs **80**:401-422.

Lane, C., S. J. Wright, J. Roncal, and J. Maschinski. 2009. Characterizing Environmental Gradients and Their Influence on Vegetation Zonation in a Subtropical Coastal Sand Dune System. Journal of Coastal Research **24**:213-224.

Leatherman, S. P., K. Zhang, and B. C. Douglas. 2000. Sea level rise shown to drive coastal erosion. Eos, Transactions American Geophysical Union **81**:55-55.

LeMercier, A. 1753. The Island Sables. Boston Weekly Newsletter, Boston, MA, USA.

Luna, B. and J. Moreno. 2009. Light and nitrate effects on seed germination of Mediterranean plant species of several functional groups. Plant Ecology **203**:123-135.

Macoun, J. 1900. Sable Island. Ann. Report to the Can. Geographical Survey.

Maechler, M., P. Rousseeuw, A. Struyf, and M. Hubert. 2005. Cluster Analysis Basics and Extensions.

Marshall, J. K. 1965. *Corynephorus Canescens* (L.) P. Beauv. as a Model for the *Ammophila* Problem. Journal of Ecology **53**:447-463.

Maun, M. A. 1994. Adaptations enhancing survival and establishment of seedlings on coastal dune systems. Plant Ecology **111**:59-70.

Maun, M. A. 1998. Adaptations of plants to burial in coastal sand dunes. Canadian Journal of Botany **713-738**.

Maun, M. A. and J. Lapierre. 1984. The Effects of Burial by Sand on *Ammophila Breviligulata*. Journal of Ecology **72**:827-839.

McCune, B. and J. B. Grace. 2002. Analysis of Ecological Communities. MjM Software Design, Durham, NC.

McCune, B. and M. J. Mefford. 2011. Multivariate Analysis of Ecological Data. MjM Software, Gleneden Beach, Oregon, U.S.A.

McInnes, K. L. 2003. Impact of sea-level rise and storm surges on a coastal community. Natural hazards **30**:187.

McNaughton, S. J. 1983. Serengeti Grassland Ecology: The Role of Composite Environmental Factors and Contingency in Community Organization. Ecological Monographs **53**:291-320.

Metropolis, N. and S. Ulam. 1949. The Monte Carlo Method. Journal of the American Statistical Association **44**:335-341.

Michener, W. K. B., Elizabeth R.; Bildstein, Keith L.; Brinson, Mark M.; Gardner, Leonard R. 1997. Climate change, hurricanes and tropical storms, and rising sea level in coastal wetlands. Ecological Applications **7**:770-801.

Mielke, P. W., K. J. Berry, P. J. Brockwell, and J. S. Williams. 1981. A Class of Nonparametric Tests Based on Multiresponse Permutation Procedures. Biometrika **68**:720-724.

Miyanishi, K. and E. A. Johnson. 2007. Coastal dune succession and the reality of dune processes. Pages 249-282 *in* A. J. Edward and M. Kiyoko, editors. Plant Disturbance Ecology. Academic Press, Burlington.

Moreno-Casasola, P. 1988. Patterns of Plant Species Distribution on Coastal Dunes Along the Gulf of Mexico. Journal of Biogeography **15**:787-806.

Noy-Meir, I. and M. Sternberg. 1999. Grazing and fire response, and plant functional types in Mediterranean grasslands. Pages 916–921 *in* D. a. D. F. Eldridge, editor. People and rangelands: building the future. Proceedings of the VIth International Rangeland Congress, Townsville, Australia.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2011. vegan: Community Ecology Package.

Pethick, J. S. 1984. An introduction to coastal geomorphology. Edward Arnold Publishers, Baltimore, MD.

Podani, J. 2005. Multivariate exploratory analysis of ordinal data in ecology: Pitfalls, problems and solutions. Journal of Vegetation Science **16**:497-510.

R Core Development Team. 2010. R: a language and environment for statistical computing.*in* R. F. f. S. Computing, editor., Vienna, Austria.

Raunkiær, C. 1905. Types biologiques pour la géographie botanique. Pages 347-438. Oversigt over Det Kongelige Danske Videnskabernes Selskabs Forhandlinger.

Roman, C. T. and K. F. Nordstrom. 1988. The effect of erosion rate on vegetation patterns of an east coast barrier island. Estuarine, Coastal and Shelf Science **26**:233-242.

Rosenzweig, M. L. 1981. A Theory of Habitat Selection. Ecology **62**:327-335.

Rosenzweig, M. L. 1991. Habitat Selection and Population Interactions: The Search for Mechanism. The American Naturalist **137**:S5-S28.

Ross, H. A. 1980. Growth of Nestling Ipswich Sparrows in Relation to Season, Habitat, Brood Size, and Parental Age. The Auk **97**:721-732.

Salisbury, E. 1952. Downs and dunes: their plant life and its environment. G. Bell and Sons, Ltd., London, England.

Seliskar, D. M. 2003. The Response of *Ammophila breviligulata* and *Spartina patens (Poaceae)* to Grazing by Feral Horses on a Dynamic Mid-Atlantic Barrier Island. American Journal of Botany **90**:1038-1044.

Sherman, D. J. and B. O. Bauer. 1993. Dynamics of beach-dune systems. Progress in Physical Geography **17**:413-447.

Silva, G. M. d., P. Hesp, J. Peixoto, and S. R. Dillenburg. 2008. Foredune vegetation patterns and alongshore environmental gradients: Moçambique Beach, Santa Catarina Island, Brazil. Earth Surface Processes and Landforms **33**:1557-1573.

St. John, H. 1921. Sable Island, with a catalogue of its vascular plants. Proceedings Boston Society of Natural History **36**.

Stalter, R. and E. E. Lamont. 2006. The Historical and Extant Flora of Sable Island, Nova Scotia, Canada. Journal of the Torrey Botanical Society **133**:362-374.

Stilwell, R. 2001. The ethos of voice in the journal of James Rainstorpe Morris from the Sable Island Humane Station, 1801-1802. Edwin Mellen Press.

Tansley, A. G. 1949. The British Islands and their vegetation. Cambridge, University Press.

Therneau, T. M., B. Atkinson, and B. Ripley. 2010a. rpart: Recursive Partitioning.

Therneau, T. M., B. Atkinson, B. Ripley, J. Oksanen, and G. De'ath. 2010b. mvpart: Multivariate partitioning.

Trabaud, L. 1987. Natural and prescribed fire: survival strategies of plants and equilibrium in mediterranean ecosystems. Pages 607-621 *in* J. D. Tenhunen, F. M. Catarino, O. L. Lange, and W. C. Oechel, editors. Plant response to stress. Functional analysis in Mediterranean ecosystems. .

van der Valk, A. G. 1974. Environmental factors controlling the distribution of forbs on coastal sand dunes in Cape Aterras National Seashore. CAN. J. BOT. **52**.

Venables, W. N. and B. D. Ripley. 2002. Modern Applied Statistics with S. Fourth edition. Springer, New York.

Vendramini, F., S. Díaz, D. E. Gurvich, P. J. Wilson, K. Thompson, and J. G. Hodgson. 2002. Leaf traits as indicators of resource-use strategy in floras with succulent species. New Phytologist **154**:147-157.

Walker, L. R. 2005. Restoring soil and ecosystem processes. Pages 192–196 *in* S. Mansourian, D.Vallauri, and N. Dudley, editors. Forest Restoration in Landscapes: Beyond Planting Trees. Springer, New York.

Ward, J. H. 1963. Hierarchical grouping to optimise an objective function. Journal of the American Statistical Association **58**:236-244.

Welsh, A. H., R. B. Cunningham, C. F. Donnelly, and D. B. Lindenmayer. 1996. Modelling the abundance of rare species: statistical models for counts with extra zeros. Ecological Modelling **88**:297-308.

Welsh, D. A. 1975. Population, behavioural, and grazing ecology of the horses of Sable Island, Nova Scotia. Dalhousie University.

Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. Plant and Soil **199**:213-227.

Woolard, J. W. and J. D. Colby. 2002. Spatial characterization, resolution, and volumetric change of coastal dunes using airborne LIDAR: Cape Hatteras, North Carolina. Geomorphology **48**:269-287.

Zimmerman, G. M., H. Goetz, and P. W. Mielke, Jr. 1985. Use of an Improved Statistical Method for Group Comparisons to Study Effects of Prairie Fire. Ecology **66**:606-611.

APPENDIX A: SPECIES ABUNDANCE

Appendix A.1 (following pages): Species abundance (0–16) for every plot sampled (*n* = 134). Species beginning with the letters A–M are represented in this table (n = 17 out of 34 total species). See Appendix A.2 for species abundances for species beginning with letters N – Z. Plot names are represented by number and letter combinations: first number is the section (1–8), second number is the transect (1–3, except for a fourth transect in section 8), the remaining letters or numbers represent the island zones (nns = north near shore, nfs = north far shore, sns = south near shore, sfs = south far shore, c1 through c4 = first through fourth center sections)

Plot	*Achillea millefolium*	*Ammophila breviligulata*	*Anaphalis margaritacea*	*Cakile edentula*	*Calluna vulgaris*	*Empetrum nigrum*	*Festuca rubra*	*Fragaria virginiana*	*Honckenya peploides*	*Spergularia salina*	*Juncus arcticus var. balticus*	*Juniperus communis var. megistocarpa*	*Juniperus horizontalis*	*Lathyrus japonicus var. maritimus*	*Maianthemum stellatum*	*Moehringia lateriflora*	*Myrica pensylvanica*
11nfs	0	7	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0
11nns	0	16	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0
11sfs	0	15	0	0	0	0	0	0	3	0	0	0	0	16	0	0	0
11sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12nfs	0	16	0	0	0	0	0	0	14	0	0	0	0	13	0	0	0
12nns	0	16	0	0	0	0	0	0	14	0	0	0	0	13	0	0	0
12sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13nfs	9	16	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0
13nns	1	16	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0
13sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21c1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21c2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21c3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21nfs	0	16	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
21nns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21sfs	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22c1	8	16	2	0	0	0	0	0	0	0	0	0	0	16	4	0	0
22nfs	3	0	0	0	0	0	16	16	0	0	12	0	0	0	9	2	6
22nns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22sfs	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0
22sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23nfs	13	16	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0
23nns	12	16	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0
23sfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Plot	*Achillea millefolium*	*Ammophila breviligulata*	*Anaphalis margaritacea*	*Cakile edentula*	*Calluna vulgaris*	*Empetrum nigrum*	*Festuca rubra*	*Fragaria virginiana*	*Honckenya peploides*	*Spergularia salina*	*Juncus arcticus var. balticus*	*Juniperus communis var. megistocarpa*	*Juniperus horizontalis*	*Lathyrus japonicus var. maritimus*	*Maianthemum stellatum*	*Moehringia lateriflora*	*Myrica pensylvanica*
23sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31c1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31c2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31c3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31nfs	8	16	0	0	0	0	16	5	0	0	0	0	0	1	0	0	0
31nns	5	16	0	0	0	0	0	0	0	0	0	0	0	13	0	0	0
31sfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32c1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32c2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32c3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32c4	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32nfs	0	16	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0
32nns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32sfs	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
32sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33c1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33c2	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33c3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33nfs	1	8	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0
33nns	2	16	0	0	0	0	15	0	0	0	0	0	0	0	0	0	0
33sfs	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
41c1	7	12	2	0	0	0	3	0	0	0	0	0	0	0	3	0	2
41c2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Plot	*Achillea millefolium*	*Ammophila breviligulata*	*Anaphalis margaritacea*	*Cakile edentula*	*Calluna vulgaris*	*Empetrum nigrum*	*Festuca rubra*	*Fragaria virginiana*	*Honckenya peploides*	*Spergularia salina*	*Juncus arcticus var. balticus*	*Juniperus communis var. megistocarpa*	*Juniperus horizontalis*	*Lathyrus japonicus var. maritimus*	*Maianthemum stellatum*	*Moehringia lateriflora*	*Myrica pensylvanica*
41c3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
41nfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
41nns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
41sfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
41sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42c1	5	3	3	0	0	8	7	4	0	0	0	0	0	0	0	0	16
42c2	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42c3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42nfs	0	13	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
42nns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42sfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
43c1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
43c2	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
43c3	0	16	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
43c4	15	15	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0
43nfs	11	12	0	0	0	0	4	0	0	0	0	0	0	14	0	0	0
43nns	0	16	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0
43sfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
43sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
51c1	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
51c2	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
51c3	6	16	6	0	0	0	16	0	0	0	0	0	0	0	2	0	13
51nfs	5	15	0	0	0	0	2	0	0	0	0	0	0	3	0	0	0
51nns	0	16	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0

Plot	*Achillea millefolium*	*Ammophila breviligulata*	*Anaphalis margaritacea*	*Cakile edentula*	*Calluna vulgaris*	*Empetrum nigrum*	*Festuca rubra*	*Fragaria virginiana*	*Honckenya peploides*	*Spergularia salina*	*Juncus arcticus var. balticus*	*Juniperus communis var. megistocarpa*	*Juniperus horizontalis*	*Lathyrus japonicus var. maritimus*	*Maianthemum stellatum*	*Moehringia lateriflora*	*Myrica pensylvanica*
51sfs	1	16	1	0	0	0	10	7	0	0	0	0	0	0	0	0	3
51sns	12	16	0	0	0	0	0	0	0	0	0	0	0	13	0	0	0
52c1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52c2	0	11	1	0	7	12	13	0	0	0	0	0	6	0	0	3	16
52c3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52nfs	1	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52nns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52sfs	3	15	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0
52sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
53c1	9	13	16	0	0	12	13	0	0	0	0	0	0	0	0	0	0
53c2	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0
53c3	0	15	0	0	0	0	1	0	0	0	0	0	0	4	0	0	0
53nfs	0	16	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0
53nns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
53sfs	0	0	0	0	0	16	16	0	0	0	0	16	2	0	0	0	15
53sns	16	16	0	0	0	0	0	0	0	0	0	0	0	8	5	0	0
61c1	1	15	1	0	0	0	10	0	0	0	8	0	0	0	0	0	0
61c2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
61c3	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
61nfs	1	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
61nns	2	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
61sfs	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
61sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
62c1	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
62c2	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Plot	*Achillea millefolium*	*Ammophila breviligulata*	*Anaphalis margaritacea*	*Cakile edentula*	*Calluna vulgaris*	*Empetrum nigrum*	*Festuca rubra*	*Fragaria virginiana*	*Honckenya peploides*	*Spergularia salina*	*Juncus arcticus var. balticus*	*Juniperus communis var. megistocarpa*	*Juniperus horizontalis*	*Lathyrus japonicus var. maritimus*	*Maianthemum stellatum*	*Moehringia lateriflora*	*Myrica pensylvanica*
62nfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
62nns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
62sfs	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
62sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
63c1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
63c2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
63c3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
63nfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
63nns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
63sfs	11	16	4	0	0	0	14	10	0	0	8	0	0	0	0	0	16
63sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
71c1	0	3	0	0	0	0	8	0	0	0	16	0	0	0	0	0	0
71c2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
71c3	0	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
71nfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
71nns	0	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
71sfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
71sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72c1	0	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72c2	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72c3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72c4	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72nfs	1	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
72nns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72sfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Plot	*Achillea millefolium*	*Ammophila breviligulata*	*Anaphalis margaritacea*	*Cakile edentula*	*Calluna vulgaris*	*Empetrum nigrum*	*Festuca rubra*	*Fragaria virginiana*	*Honckenya peploides*	*Spergularia salina*	*Juncus arcticus var. balticus*	*Juniperus communis var. megistocarpa*	*Juniperus horizontalis*	*Lathyrus japonicus var. maritimus*	*Maianthemum stellatum*	*Moehringia lateriflora*	*Myrica pensylvanica*
72sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
73nns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
73sfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
73sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
81ns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
82ns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
83ns	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0
84nns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
84sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix A.2 (following pages): Species abundance (0–16) for every plot sampled (*n* = 134). Species beginning with the letters N – Z are represented in this table (n = 17 out of 34 total species). See Appendix A.2 for species abundances for species beginning with letters A – M. Plot names are represented by number and letter combinations: first number is the section (1–8), second number is the transect (1–3, except for a fourth transect in section 8), the remaining letters or numbers represent the island zones (nns = north near shore, nfs = north far shore, sns = south near shore, sfs = south far shore, c1 through c4 = first through fourth center sections)

Plot	*Oenothera parviflora*	*Photinia floribunda*	*Plantago lanceolata*	*Poa* spp	*Rhinanthus minor*	*Rosa virginiana*	*Rumex acetosella*	*Rumex crispus*	*Sibbaldiopsis tridentate*	*Sisyrinchium angustifolium*	*Solidago sempervirens*	*Stellaria graminea*	*Symphyotrichum novi-belgii*	*Thalictrum pubescens*	*Trientalis borealis*	*Vaccinium angustifolium*	*Vaccinium macrocarpon*
11nfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11nns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11sfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12nfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12nns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13nfs	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0
13nns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21c1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21c2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21c3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21nfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21nns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21sfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22c1	0	0	0	16	0	5	0	0	0	0	1	0	0	0	0	0	0
22nfs	0	0	0	0	2	16	0	0	0	3	0	6	1	9	0	8	0
22nns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22sfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23nfs	0	0	0	16	0	0	0	0	0	0	1	0	0	0	0	0	0
23nns	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0
23sfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31c1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31c2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Plot	*Oenothera parviflora*	*Photinia floribunda*	*Plantago lanceolata*	*Poa* spp	*Rhinanthus minor*	*Rosa virginiana*	*Rumex acetosella*	*Rumex crispus*	*Sibbaldiopsis tridentate*	*Sisyrinchium angustifolium*	*Solidago sempervirens*	*Stellaria graminea*	*Symphyotrichum novi-belgii*	*Thalictrum pubescens*	*Trientalis borealis*	*Vaccinium angustifolium*	*Vaccinium macrocarpon*
31c3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31nfs	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0
31nns	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
31sfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32c1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32c2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32c3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32c4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32nfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32nns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32sfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33c1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33c2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33c3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33nfs	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0
33nns	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0
33sfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
41c1	0	0	0	4	0	2	0	0	0	0	0	0	0	0	0	0	0
41c2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
41c3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
41nfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
41nns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
41sfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
41sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42c1	0	3	0	0	0	11	12	0	0	0	0	0	12	0	4	16	0

Plot	*Oenothera parviflora*	*Photinia floribunda*	*Plantago lanceolata*	*Poa* spp	*Rhinanthus minor*	*Rosa virginiana*	*Rumex acetosella*	*Rumex crispus*	*Sibbaldiopsis tridentate*	*Sisyrinchium angustifolium*	*Solidago sempervirens*	*Stellaria graminea*	*Symphyotrichum novi-belgii*	*Thalictrum pubescens*	*Trientalis borealis*	*Vaccinium angustifolium*	*Vaccinium macrocarpon*
42c2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42c3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42nfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42nns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42sfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
43c1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
43c2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
43c3	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
43c4	0	0	0	16	0	4	0	0	0	0	0	0	0	0	0	0	0
43nfs	0	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0
43nns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
43sfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
43sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
51c1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
51c2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
51c3	0	0	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0
51nfs	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
51nns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
51sfs	6	0	0	0	0	0	13	0	0	0	0	0	0	0	0	0	1
51sns	0	0	0	16	0	0	0	0	0	0	3	0	0	0	0	0	0
52c1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52c2	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	11	4
52c3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52nfs	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0
52nns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52sfs	0	0	0	0	0	0	0	0	0	0	14	0	0	0	0	0	0
52sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Plot	*Oenothera parviflora*	*Photinia floribunda*	*Plantago lanceolata*	*Poa* spp	*Rhinanthus minor*	*Rosa virginiana*	*Rumex acetosella*	*Rumex crispus*	*Sibbaldiopsis tridentate*	*Sisyrinchium angustifolium*	*Solidago sempervirens*	*Stellaria graminea*	*Symphyotrichum novi-belgii*	*Thalictrum pubescens*	*Trientalis borealis*	*Vaccinium angustifolium*	*Vaccinium macrocarpon*
53c1	0	0	0	0	2	7	0	0	16	0	0	0	8	0	0	10	0
53c2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
53c3	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0
53nfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
53nns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
53sfs	0	0	0	0	0	0	0	0	8	0	0	0	1	0	0	2	0
53sns	0	0	0	16	0	13	0	0	0	0	11	0	0	0	0	0	0
61c1	1	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0
61c2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
61c3	4	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
61nfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
61nns	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0
61sfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
61sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
62c1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
62c2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
62nfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
62nns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
62sfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
62sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
63c1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
63c2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
63c3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
63nfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
63nns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
63sfs	0	0	0	0	0	4	1	0	0	0	13	0	14	0	0	0	0
63sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
71c1	3	0	0	3	0	0	0	0	0	0	4	0	0	0	0	0	0

Plot	*Oenothera parviflora*	*Photinia floribunda*	*Plantago lanceolata*	*Poa* spp	*Rhinanthus minor*	*Rosa virginiana*	*Rumex acetosella*	*Rumex crispus*	*Sibbaldiopsis tridentate*	*Sisyrinchium angustifolium*	*Solidago sempervirens*	*Stellaria graminea*	*Symphyotrichum novi-belgii*	*Thalictrum pubescens*	*Trientalis borealis*	*Vaccinium angustifolium*	*Vaccinium macrocarpon*
71c2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
71c3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
71nfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
71nns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
71sfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
71sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72c1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72c2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72c3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72c4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72nfs	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
72nns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72sfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
73nns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
73sfs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
73sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
81ns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
82ns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
83ns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
84nns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
84sns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX B: ENVIRONMENTAL VARIABLES AND PLOT LOCATIONS

Appendix B.1 (following pages): Location and environmental variables for every plot sampled (*n* = 134). Plot names are represented by number and letter combinations: first number is the section (1–8), second number is the transect (1–3, except for a fourth transect in section 8), the remaining letters or numbers represent the island zones (nns = north near shore, nfs = north far shore, sns = south near shore, sfs = south far shore, c1 through c4 = first through fourth center sections). Northing, easting, and elevation were taken with hand held GPS. Slope was measured using an inclinometer, and aspects were measures using a compass. Folded aspects (*Af.*) along the north-south (*NS*) line were calculated as: $Af.NS = 180 - |aspect - 180|$. Folded aspects along the east-west (EW) line were calculated as: $.EW = Af.NS + 90$. Aspects that had no values because zero slopes were changed to the mean value of each folded aspect. Orientation was devised and used as north facing = 1, flat = 0, and south facing = -1.

plot	northing	easting	elevation	slope	Af.NS	Af.EW	orientation	m from south shore	m from north shore	organic layer	plot position	site contour	grazing evidence
11nfs	43.95477	60.12074	0	10	40	130	1	254	143	0	7	4	3
11nns	43.95585	60.12099	5	6	2	92	1	329	58	0	2	2	4
11sfs	43.95343	60.12004	11	8	43	133	1	151	229	0	3	3	4
11sns	43.95208	60.1199	8	0	91	181	0	11	350	0	10	1	0
12nfs	43.96336	60.1418	9	6	38	128	1	158	195	0	7	3	2
12nns	43.96491	60.1463	13	6	42	132	1	49	190	0	1	4	4
12sns	43.96201	60.14197	7	0	91	181	0	29	337	0	10	1	0
13nfs	43.93682	60.0689	19	2	15	105	1	75	146	0	3	4	4
13nns	43.93763	60.06901	12	4	42	132	1	166	62	0	3	4	4
13sns	43.93615	60.06875	12	3	140	230	-1	2	215	0	10	2	0
21c1	43.93235	59.99169	7	0	91	181	0	680	367	0	6	1	0
21c2	43.93055	59.99116	8	0	91	181	0	486	569	0	6	1	0
21c3	43.92852	59.9911	7	0	91	181	0	262	794	0	6	1	0
21nfs	43.93472	59.99258	14	8	48	138	1	939	95	0	3	1	4
21nns	43.9356	59.99282	8	6	8	98	1	1037	2	0	3	1	0
21sfs	43.92804	59.99104	5	0	91	181	0	211	847	0	6	1	0
21sns	43.92688	59.99087	9	0	91	181	0	93	975	0	6	1	0
22c1	43.93315	60.01645	14	5	129	219	-1	601	217	0	4	3	4
22nfs	43.93122	60.0164	11	2	173	263	-1	391	431	1	3	4	4
22nns	43.93494	60.01653	10	1	162	252	-1	796	18	0	10	1	0
22sfs	43.92994	60.01621	12	0	91	181	0	253	574	0	6	1	0
22sns	43.92822	60.0165	1	0	91	181	0	61	762	0	10	1	0
23nfs	43.93388	60.04272	17	11	180	270	-1	319	178	0	2	2	3
23nns	43.93457	60.04277	21	7	48	138	1	394	104	0	7	4	4
23sfs	43.93311	60.04273	11	0	91	181	0	235	262	0	10	1	0
23sns	43.93109	60.04262	12	12	146	236	-1	23	482	0	10	1	0
31c1	43.93324	59.98368	7	0	91	181	0	812	298	0	10	1	0
31c2	43.93085	59.98335	4	0	91	181	0	545	563	0	10	1	0
31c3	43.92947	59.9833	8	0	91	181	0	393	716	0	10	1	0
31nfs	43.93419	59.9838	14	4	140	230	-1	918	192	0	1	4	1
31nns	43.93527	59.98399	17	9	120	210	-1	1039	72	0	1	4	0

plot	northing	easting	elevation	slope	Af.NS	Af.EW	orientation	m from south shore	m from north shore	organic layer	plot position	site contour	grazing evidence
31sfs	43.92801	59.98315	6	0	91	181	0	232	877	0	10	1	0
31sns	43.92693	59.98303	4	0	91	181	0	113	997	0	10	1	0
32c1	43.92828	59.94688	8	0	91	181	0	291	909	0	10	1	0
32c2	43.93095	59.9472	21	5	52	142	1	585	613	0	9	3	1
32c3	43.93282	59.94747	15	5	160	250	-1	792	406	0	3	1	0
32c4	43.93335	59.94748	19	3	35	125	1	850	347	0	7	3	2
32nfs	43.93478	59.94756	21	5	98	188	-1	1009	188	0	7	4	0
32nns	43.93628	59.94755	9	1	170	260	-1	1176	21	0	10	1	0
32sfs	43.92704	59.94675	6	0	91	181	0	154	1047	0	10	1	0
32sns	43.92651	59.94667	7	0	91	181	0	95	1106	0	10	1	0
33c1	43.92874	59.96195	9	0	91	181	0	353	813	0	10	1	0
33c2	43.93008	59.96203	11	5	128	218	-1	501	664	0	4	3	4
33c3	43.93323	59.96228	11	40	153	243	-1	849	314	0	9	1	0
33nfs	43.93483	59.96258	9	22	130	220	-1	1024	136	0	3	4	0
33nns	43.93535	59.96264	17	26	4	94	1	1082	79	0	3	4	0
33sfs	43.9271	59.96186	5	8	168	258	-1	175	995	0	4	3	3
33sns	43.92638	59.96181	10	0	91	181	0	101	1075	0	10	1	0
41c1	43.93319	59.89541	12	5	140	230	-1	767	429	0	5	4	4
41c2	43.93156	59.89486	8	9	160	250	-1	582	615	0	4	3	0
41c3	43.9277	59.89353	11	0	91	181	0	146	1057	0	10	1	0
41nfs	43.93498	59.89625	18	27	172	262	-1	968	221	0	3	1	0
41nns	43.93681	59.89706	9	6	10	100	1	1171	13	0	10	2	0
41sfs	43.92786	59.89273	10	0	91	181	0	160	1050	0	10	1	0
41sns	43.92673	59.89223	9	0	91	181	0	32	1176	0	10	1	0
42c1	43.93396	59.89122	3	2	160	250	-1	801	387	1	7	4	4
42c2	43.93253	59.89104	9	2	158	248	-1	643	546	0	4	1	2
42c3	43.93066	59.89095	8	0	91	181	0	438	752	0	10	1	0
42nfs	43.93625	59.89141	13	5	155	245	-1	1053	142	0	7	3	4
42nns	43.93692	59.89141	10	1	54	144	1	1126	73	0	4	1	0
42sfs	43.92861	59.89094	6	0	91	181	0	217	978	0	10	1	0
42sns	43.92686	59.89086	9	4	0	90	1	28	1172	0	10	1	0

plot	northing	easting	elevation	slope	Af.NS	Af.EW	orientation	m from south shore	m from north shore	organic layer	plot position	site contour	grazing evidence
43c1	43.93056	59.88601	10	0	91	181	0	350	825	0	10	1	0
43c2	43.93304	59.88619	12	8	22	112	1	625	554	0	3	4	1
43c3	43.93358	59.88617	12	7	78	168	1	684	497	0	2	2	3
43c4	43.93577	59.88651	16	4	148	238	-1	928	260	0	7	4	4
43nfs	43.93621	59.88652	16	4	26	116	1	977	213	0	7	3	4
43nns	43.93764	59.88669	15	7	15	105	1	1136	57	0	3	4	2
43sfs	43.92885	59.88594	6	0	91	181	0	162	1013	0	10	1	0
43sns	43.92791	59.88589	9	0	91	181	0	59	1117	0	10	1	0
51c1	43.93694	59.87086	20	8	135	225	-1	804	346	0	2	4	4
51c2	43.93419	59.87083	16	3	112	202	-1	501	647	0	7	4	3
51c3	43.93312	59.8701	18	8	78	168	1	376	774	1	2	4	4
51nfs	43.93891	59.87135	12	4	170	260	-1	1026	123	0	3	2	4
51nns	43.93965	59.8714	11	9	28	118	1	1109	42	0	2	3	4
51sfs	43.93143	59.87083	14	2	19	109	1	202	951	0	9	3	4
51sns	43.93031	59.87073	13	12	28	118	1	79	1075	1	3	3	4
52c1	43.93026	59.88099	7	0	91	181	0	261	947	0	8	1	0
52c2	43.93259	59.88105	13	12	25	115	1	512	693	0	7	4	4
52c3	43.93527	59.8812	18	34	118	208	-1	804	402	0	9	1	0
52nfs	43.93716	59.8816	12	5	125	215	-1	1009	189	0	7	2	0
52nns	43.93905	59.88152	8	9	5	95	1	1204	5	0	10	1	0
52sfs	43.92903	59.88092	15	7	125	215	-1	128	1082	0	2	2	0
52sns	43.92814	59.88081	7	0	91	181	0	32	1181	0	10	1	0
53c1	43.93407	59.85931	12	5	68	158	1	307	832	1	7	4	4
53c2	43.93653	59.85974	7	1	65	155	1	582	558	0	7	1	3
53c3	43.9389	59.86028	14	2	138	228	-1	849	291	0	7	1	4
53nfs	43.93983	59.86033	17	3	70	160	1	952	190	0	2	4	4
53nns	43.94152	59.86051	7	7	10	100	1	1135	6	0	10	1	0
53sfs	43.9329	59.85921	9	3	30	120	1	179	961	0	7	1	4
53sns	43.93221	59.85911	10	4	0	90	1	103	1037	1	4	1	4
61c1	43.95349	59.8041	10	0	39	129	0	644	276	0	7	4	3
61c2	43.95263	59.80382	11	20	141	231	-1	547	372	0	9	1	0

plot	northing	easting	elevation	slope	Af.NS	Af.EW	orientation	m from south shore	m from north shore	organic layer	plot position	site contour	grazing evidence
61c3	43.95004	59.8023	16	12	129	219	-1	234	685	0	1	2	0
61nfs	43.95468	59.80453	26	2	136	226	-1	780	141	0	1	4	0
61nns	43.95522	59.80482	27	9	18	108	1	844	77	0	1	4	0
61sfs	43.94919	59.8019	8	0	91	181	0	134	784	0	10	1	0
61sns	43.94851	59.80155	9	0	91	181	0	54	865	0	10	1	0
62c1	43.94295	59.82547	8	4	65	155	1	389	639	0	5	3	0
62c2	43.94654	59.82587	2	3	78	168	1	748	265	0	7	4	2
62nfs	43.94775	59.82597	11	3	0	90	1	871	139	0	9	1	0
62nns	43.94822	59.82604	8	0	91	181	0	921	89	0	10	1	0
62sfs	43.94046	59.8254	15	9	180	270	-1	131	905	0	2	2	0
62sns	43.93945	59.82528	7	1	180	270	-1	24	1013	0	10	1	0
63c1	43.94268	59.83795	11	3	154	244	-1	730	312	0	4	1	0
63c2	43.94146	59.83788	9	1	110	200	-1	599	442	0	9	1	0
63c3	43.93976	59.83779	16	3	86	176	1	420	628	0	9	1	0
63nfs	43.9437	59.83801	16	0	91	181	0	841	205	0	9	1	0
63nns	43.94544	59.83815	11	1	35	125	1	1032	32	0	10	1	0
63sfs	43.93793	59.8376	11	6	78	168	1	228	829	0	7	4	4
63sns	43.93641	59.83764	16	38	180	270	-1	79	994	0	3	1	0
71c1	43.95547	59.79974	9	7	152	242	-1	691	222	0	8	1	4
71c2	43.95374	59.79945	0	0	91	181	0	515	410	0	5	1	0
71c3	43.95176	59.79951	18	13	175	265	-1	317	605	0	2	1	4
71nfs	43.95624	59.79982	10	2	20	110	1	766	144	0	9	1	0
71nns	43.95696	59.79972	29	12	18	108	1	832	80	0	3	4	4
71sfs	43.95052	59.79947	8	0	91	181	0	190	733	0	10	1	0
71sns	43.94919	59.79929	5	0	91	181	0	54	876	0	10	1	0
72c1	43.95993	59.78642	15	5	32	122	1	573	319	0	3	1	1
72c2	43.95898	59.78642	23	3	162	252	-1	489	410	0	1	4	4
72c3	43.95467	59.7862	5	0	91	181	0	104	821	0	10	1	0
72c4	43.95672	59.78621	13	11	105	195	-1	283	625	0	9	3	4
72nfs	43.9613	59.7866	29	34	40	130	1	704	187	0	3	4	0
72nns	43.96305	59.78673	10	4	35	125	1	869	6	0	10	1	0

plot	northing	easting	elevation	slope	Af.NS	Af.EW	orientation	m from south shore	m from north shore	organic layer	plot position	site contour	grazing evidence
72sfs	43.95576	59.78616	10	0	91	181	0	196	719	0	10	1	0
72sns	43.95447	59.7862	5	0	91	181	0	87	840	0	10	1	0
73nns	43.98295	59.75166	9	0	91	181	0	243	31	0	10	1	0
73sfs	43.98203	59.75167	0	0	91	181	0	170	103	0	10	1	0
73sns	43.98009	59.75155	8	3	125	215	-1	11	279	0	10	1	0
81ns	44.03547	59.66491	9	0	91	181	0	106	38	0	10	1	0
82ns	44.02765	59.679	7	0	91	181	0	44	53	0	10	1	0
83ns	44.02028	59.69234	11	0	91	181	0	150	47	0	10	4	0
84nns	44.02371	59.68614	9	2	160	250	-1	88	37	0	10	1	0
84sns	44.02279	59.68609	10	2	25	115	1	9	123	0	10	1	0

APPENDIX C: PLANT TRAITS

Appendix C.1 (following pages): Table of plant traits for species that occurred at least twice in sampling plots. Height data was calculated as the average of five randomly selected individuals to the nearest cm. All other traits were determined in the field and from Manual of Vascular Plants of Northeastern United States and Adjacent Canada (Gleason and Cronquist 1991).

Species	life form	perennial	ramets	height (cm)	creeping or fibrous roots	trichomes	waxy or succulent leaves
Achillea millefolium	geophyte	1	dispersed	35	0	1	0
Ammophila breviligulata	hemicryptophyte	1	clumped	104	1	0	0
Anaphalis margaritacea	geophyte	1	dispersed	16	1	1	0
Cakile edentula	therophyte	0	spreading	25	1	0	1
Calluna vulgaris	chamaephyte	1	clumped	25	1	0	0
Empetrum nigrum	chamaephytes	1	spreading	8	0	0	0
Festuca rubra	hemicryptophyte	1	clumped	20	1	0	0
Fragaria virginiana	hemicryptophyte	1	spreading	6	1	1	0
Honckenya peploides	geophyte	1	spreading	21	1	0	1
Juncus arcticus* var. *balticus	geophyte	1	dispersed	50	1	0	0
Juniperus communis* var. *megistocarpa	phaneropyte	1	spreading	12	0	0	1
Juniperus horizontalis	chamaephyte	1	spreading	5	0	0	1
Lathyrus japonicus* var. *maritimus	geophyte	1	spreading	37	0	0	1
Maianthemum stellatum	phaneropyte	1	dispersed	16	1	0	1
Moehringia lateriflora	hemicryptophyte	1	spreading	23	1	1	0
Myrica pensylvanica	chamaephyte	1	clumped	22	0	0	1
Oenothera parviflora	therophyte	1	dispersed	28	0	0	0
Photinia floribunda	phaneropyte	1	clumped	15	1	1	0
Plantago lanceolata	hemicryptophyte	1	dispersed	25	1	1	0
***Poa* spp**	hemicryptophyte	1	clumped	20	1	0	0
Rhinanthus minor	therophyte	0	spreading	26	1	1	0
Rosa virginiana	phaneropyte	1	clumped	29	1	1	0
Rumex acetosella	geophyte	1	clumped	9	1	0	0
Rumex crispus	hemicryptophyte	1	dispersed	74	0	0	0
Sibbaldiopsis tridentate	hemicryptophyte	1	spreading	7	1	1	1
Solidago sempervirens	hemicryptophyte	1	clumped	59	0	0	1
Spergularia salina	therophyte	0	clumped	2	1	0	0
Stellaria graminea	hemicryptophyte	1	dispersed	11	1	1	0
Symphyotrichum novi-belgii	hemicryptophyte	1	dispersed	11	1	0	0
Thalictrum pubescens	hemicryptophyte	1	dispersed	22	1	1	0
Trientalis borealis	geophyte	1	spreading	6	1	0	0
Vaccinium angustifolium	chamaephyte	1	clumped	9	1	0	0
Vaccinium macrocarpon	chamaephyte	1	spreading	2	1	0	0